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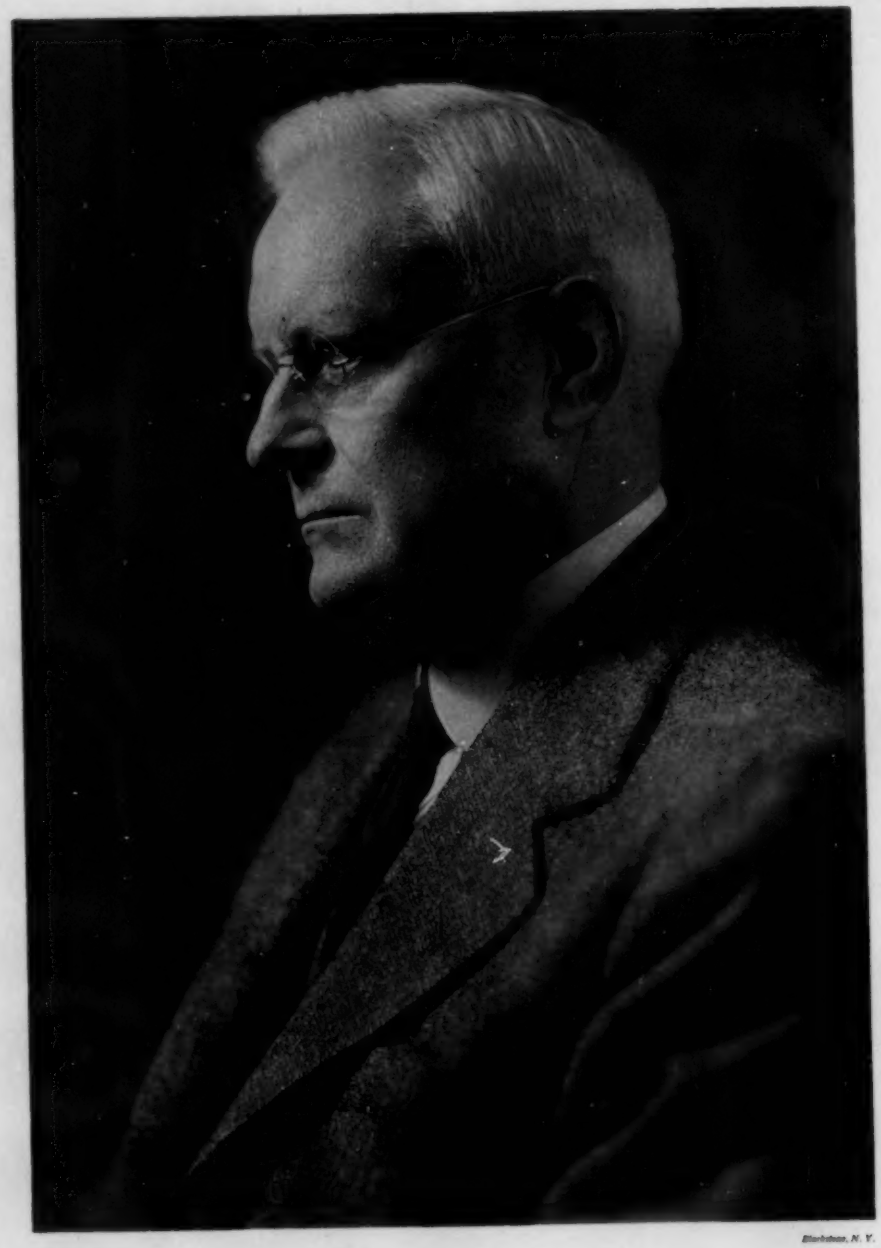

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CHARLES STUART GAGER

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 71, NO. 3, PP. 193–198 MAY, 1944

C. STUART GAGER

December 23, 1872—August 9, 1943

GEORGE M. REED AND ARTHUR H. GRAVES[1]

Charles Stuart Gager, the son of Charles Carroll and Leora Josephine (Darke) Gager, was born at Norwich, N. Y., where he spent his boyhood and obtained his elementary education in the local public schools. In the fall of 1891 he attended Syracuse University, graduating with the A.B. degree in 1895. During his senior year he served as undergraduate laboratory assistant in the Department of Biology, which was in charge of Dr. Charles W. Hargitt.

Following his graduation from Syracuse University, Dr. Gager was for one year (1895–1896) Vice Principal of the Ives Seminary, Antwerp, N. Y. The next year (1896–1897) he attended the New York State Normal College, Albany, N. Y., and obtained the two degrees, Bachelor and Master of Pedagogy. In the fall of 1897 he became Professor of Biological Sciences and Physiography at this institution, holding the position until September, 1904. During this period, however, he attended the Harvard Summer School in 1898, served as Assistant in Botany at Cornell University (1901–1902), and Instructor in Botany during the summer of 1904. He was Laboratory Assistant at the New York Botanical Garden (1904–1905), and in the spring of 1905 he was Acting Professor of Botany at Rutgers College, N. J. In the fall of 1905 he was teacher of Botany in the Morris High School, N. Y. He also taught Botany in the summer sessions of New York University in 1905 and 1906. He obtained his degree of Doctor of Philosophy at Cornell University in 1902, carrying on his research under the direction of Professor George F. Atkinson, his doctoral thesis being concerned with "The Development of the Pollinium and Sperm-Cells in *Asclepias Cornuti* Decaisne."

On February 1, 1906, Dr. Gager became Director of the Laboratories at the New York Botanical Garden, succeeding Dr. Daniel Trembly MacDougal, and holding this position until August, 1908. While at the Garden he devoted himself largely to research, making a special study of the effects of the rays of radium on plants. The results of his investigations were published in 1908 as a Memoir of the New York Botanical Garden. His interest in this subject continued throughout his life. He cooperated in 1927 with Dr. A. F. Blakeslee on the use of rays of radium for inducing chromosome and gene mutations in *Datura*. As recently as 1936 he prepared a chapter, "The Effects

[1] The portrait of Dr. Gager is published at the expense of the Lucien M. Underwood Memorial Fund.

[THE BULLETIN for March (71: 107–192) was issued March 1, 1944.]

of Radium Rays on Plants, A Brief Résumé of the More Important Papers from 1901 to 1932," which was published in *Biological Effects of Radiation,* edited by Professor B. M. Duggar. Also, while he was at the New York Botanical Garden he was occupied with his translation of DeVries' work on *Intracellular Pangenesis,* which he published in 1910.

Beginning in September, 1908, for two years Dr. Gager was Professor of Botany at the University of Missouri, serving as Administrative Chairman of the department. He was in charge of the general course in botany, also teaching advanced courses in physiology and morphology. A large number of students registered for the general course at the University, mostly freshmen or sophomores in the College of Agriculture or the College of Arts and Sciences. His teaching experience during these two years led him to the preparation of his text book *The Fundamentals of Botany,* published in 1916. Accompanying this text *A Laboratory Outline in General Botany* was published, the first edition appearing in 1916, the second in 1919, and the third in 1926. He further contributed to botanical text books by publishing, in 1926, his *General Botany with Special Reference to Its Economic Aspects.*

On the first of July, 1910, Dr. Gager took up the work as Director of the newly established Brooklyn Botanic Garden, and for more than thirty-three years guided its destinies. During the earlier years he was closely associated with Mr. Alfred T. White, who is recognized as the "Father" of the Garden, and was the chief inspiration and support in the founding and early development.

Dr. Gager thought of a botanic garden as something quite different from the traditional type. His motto for the Brooklyn Botanic Garden was "For the Service of the City and the Advancement of Botany," and to him this ideal meant beautiful grounds with displays of both botanical and popular value and interest, botanical research, and public education, all of which are reflected in the history and development of the Brooklyn Botanic Garden. He laid particular emphasis upon the possibilities of botanical education as an important part of a botanic garden's activities. This led to the establishment of the curatorship of Public Instruction in 1912, and in 1913 an instructorship in this department with special supervision of the educational work for children, this phase being separated in 1916 as the Department of Elementary Instruction. The educational work with children is one of the outstanding features of the Garden's activities, for which it is widely and favorably known.

Further, Dr. Gager thought of a botanic garden as an outdoor museum of living plants. He strongly emphasized not only the botanical aspects, but the horticultural as well, stressing the value of building up horticultural collections. Thus, in the course of time, special features—*Gardens Within a Garden*—were developed. One of the earliest was the establishment of the

Local Flora, an area set aside for growing native plants that are found within one hundred miles of New York City. The *Japanese Landscape Garden* was first opened to the public on June 5, 1915, and the *Rock Garden* in the spring of 1917. The *Children's Gardens,* together with the *Children's House* were completed for use in 1916. The *Rose Garden* was opened to the public in 1927, and the *Herb Garden* and *Medicinal Plant Garden* were established in 1938.

When Dr. Gager first came to Brooklyn he had a small office space in the Academy of Music and, later, in the Brooklyn Museum building. In the fall of 1913 the first section of the *Laboratory Building,* consisting of only a small portion of the south end of the present structure, together with the adjacent conservatories, was completed for occupancy by the staff. It was not until the spring of 1917 that the rest of the building was completed, being formally dedicated on April 19–21, the ceremonies being attended by many eminent botanists, who presented formal papers on the occasion.

Dr. Gager displayed a broad interest in botanical and horticultural affairs and was an active member of many societies. He was a member of the Botanical Society of America (President, 1936), The Torrey Botanical Club (Secretary 1905–1908, Vice President, 1917–1931, President 1942), the New York Academy of Sciences (Corresponding Secretary 1941), the Society of Experimental Biology and Medicine, American Society of Naturalists, American Society of Biological Chemists, Ecological Society of America, the Genetics Society of America, Fellow of the A.A.A.S. (Vice President and Chairman of Section G in 1917), the Horticultural Society of New York (served on the Board of Directors since 1928, and Vice Chairman since 1937). He was made an honorary life member of the Pennsylvania Horticultural Society in 1934, the School Garden Association of America, the Royal New Zealand Institute of Horticulture (1940), and the Royal Agricultural and Horticultural Society of India (1941). He was a member of Phi Beta Kappa and Sigma Xi. Among special honors that Dr. Gager received was the Arthur Hoyt Scott gold medal and cash award for outstanding achievement in the field of horticulture in 1941. In 1920 Syracuse University conferred on him the honorary degree of Doctor of Science, and in 1921 the New York State College for Teachers, the degree of Doctor of Pedagogy.

Dr. Gager served on many important committees, dealing more particularly with horticultural affairs. Among others, the Committee on Plant Quarantines and their Administration, the Committee on Botanical Exhibits for the World's Fair at Chicago in 1933, Sub-committee on Scope and Function of the Planning Committee on U. S. Botanic Gardens, Washington, D. C. (1934–1936), and the Committee of the International Flower Show (1932–). He also served on the New Jersey Federation of Shade Tree Com-

missions (1934–), and the Board of Directors, American Association of Botanical Gardens and Arboretums (1940–).

His diversified interests were evidenced by his activities on the Brooklyn Civic Council, the Park Association of New York City, and the National Institute of Social Sciences, of which he was Vice President (1928–1931), President (1932–1935), and again Vice President (1935–). He was an active member and Ruling Elder of the Reformed Protestant Dutch Church of Flatbush. He was a member of the Century Association, Twentieth Century Club (President 1933–1935), the Winter's Night Club, and the Rembrandt Club.

He took an active part in the founding and carrying on of botanical journals for the publication of scientific results. He was the first Business Manager of the *American Journal of Botany*, founded in 1914, continuing until 1935, during which time twenty-two volumes were published. He also served as Business Manager for *Ecology* from its founding in 1920, and for *Genetics* since 1922.

In 1910, soon after coming to the Garden, Dr. Gager accompanied Dr. and Mrs. N. L. Britton on a trip to Cuba. In 1927 he was in Europe for several months, visiting particularly France and Italy. This visit was primarily for the purpose of gathering data on the European Botanic Gardens, since he was then engaged in the preparation of *The Botanic Gardens of the World*, the first edition of this work being published in 1937 and the second in 1938. In 1930 he attended the Fifth International Botanical Congress in Cambridge, England, again visiting botanical gardens in several European countries.

On June 25, 1902, Dr. Gager married Bertha Woodward Bagg of Rensselaer, N. Y., who was of invaluable assistance to him throughout his career because of her tact, charm, and wise counsel. They had two children, Benjamin Stuart, who was born on January 10, 1904, and died March 31, 1918, and Prudence, now Mrs. Kenneth G. Bucklin.

Dr. Gager was much sought after as a speaker for popular addresses on botanical or horticultural subjects. He had a very attractive personality, a pleasing manner in his addresses, and always gave a clear and interesting presentation of his subject.

A selected list of the writings of C. Stuart Gager

In addition to many reviews and papers chiefly on matters of horticultural and pedagogical interest, Dr. Gager, as editor of the Brooklyn Botanic Garden Record, wrote many short articles about matters relating to the Brooklyn Botanic Garden, and, each year, an extensive report of the activities of the Garden. A list of these published writings would contain more than 300 titles. We have, therefore, gathered together and arranged in chronological order the following selected list of those papers which we believe are of special importance for botanical science.

The development of the pollinium and sperm-cells in *Asclepias Cornuti* Decaisne. A thesis submitted to the university faculty of Cornell University for the degree of Doctor of Philosophy, June, 1902. (Also Ann. Bot. **16**: 123–148. *7 pl.* Mr 1902.)

Preliminary notes on the effects of radium rays on plants. (Soc. for experimental biol. and medicine. Proceedings reported by the Secretary, W. J. Gies. May 24, 1905, p. 14.) Also Am. Medicine 9^{25}: 1030. 1905.

Tuber-formation in *Solanum tuberosum* in daylight. Torreya **6**: 181–186. S 1906.

Further note on the formation of aërial tubers in *Solanum*. Torreya **6**: 211, 212. 25 O 1906.

The breathing of plants. Jour. N. Y. Bot. Gard. **8**: 143–156. Jl 1907.

Radium in biological research. Science **25**: 589–590. 12 Ap 1907.

Effects of the rays of radium on plants. Mem. N. Y. Bot. Gard. **4**. 278 p. *14 pl.* 1908.

Some physiological effects of radium rays. Am. Nat. **42**: 761–778. *17 f.* 1908.

The influence of radium rays on a few life processes of plants. (Contr. Dept. Bot. Univ. Missouri no. 16.) Pop. Sci. Mo. **74**: 222–232. 1909.

A laboratory outline for general botany. 90 p. Columbia, Mo. 1909.

Radium rays and plant life processes. Sci. Am. Suppl. $57^{1473\text{S}}$: 264–265. *13 f.* 1909.

Vries, Hugo de. Intracellular pangenesis including a paper on fertilization and hybridization. Transl. from the German by C. Stuart Gager. 270 p. Open Court Publ. Co., Chicago. O 1910.

The Brooklyn Botanic Garden. Jour. N. Y. Bot. Gard. **11**: 190–191. Au 1910.

The educational work of botanic gardens. Cyclopedia of Education. pp. 421–425. The MacMillan Co., New York. 1911. Also in Jour. N. Y. Bot. Gard. **12**: 73–85. 1911. Reissued separately as Brooklyn Bot. Gard. Contr. no. 1.

The purpose of an introductory course in botany. Proc. 24th Ann. Convention Assoc. Coll. & Prep. Schools of Middle States & Maryland. **1910**: 58–65. 1911. Reissued as Brooklyn Bot. Gard. Contr. no. 2.

Cryptomeric inheritance in *Onagra*. Bull. Torrey Club **38**: 461–471. *pl. 20, 21.* O 1911. Reissued as Brooklyn Bot. Gard. Contr. no. 3.

The Brooklyn Botanic Garden. Pop. Sci. Mo. **80**: 338–345. Ap 1912.

The first botanic garden on Long Island. Brooklyn Bot. Gard. Record **1**: 97–99. O 1912.

Ingrowing sprouts of *Solanum tuberosum*. Bot. Gaz. **54**: 515–524. D 1912. Reissued as Brooklyn Bot. Gard. Contr. no. 5.

The opening of buds. Brooklyn Bot. Gard. Leafl. 1^{3}: Ap 1913.

The pollination of pines. Brooklyn Bot. Gard. Leafl. 1^{5}: My 1913.

Botanic Garden. *In:* L. H. Bailey, The Standard Cyclopedia of Horticulture **1**: 526–532. 1914.

The translocation of material in dying leaves. Science **41**: 99–104. 15 Ja 1915.

Present status of the problem of the effect of radium rays on plant life. Mem. N. Y. Bot. Gard. **6**: 153–160. 31 Au 1916.

Fundamentals of botany. xx + 640 p. *434 f.* P. Blakiston's Son & Co., Philadelphia. 1916.

A laboratory guide for general botany. viii + 191 p. P. Blakiston's Son & Co., Philadelphia. 17 N 1916.

Ideals and opportunities for a botanic garden. Brooklyn Bot. Gard. Record **6**: 121–130. Jl 1917.

Forest problems of the Ashokan watershed. Brooklyn Bot. Gard. Leafl. $5^{12\text{-}13}$: 10 O 1917.

The near future of botany in America. Science **47**: 101–115. 1 Fe 1918.

A brief history of the botanic garden idea in Brooklyn. Brooklyn Bot. Gard. Record **7**: 99–112. O 1918.

A laboratory guide for general botany. ed. 2. x + 206 p. P. Blakiston's Son & Co., Philadelphia. 18 Fe 1919.

Heredity and evolution in plants. xv + 265 p. *113 f.* P. Blakiston's Son & Co., Philadelphia. Au 1920.

The educational value of a botanic garden. Museum Work **7**: 3–10. My–Je 1924.

A laboratory guide for general botany. ed. 3. x + 205 p. P. Blakiston's Son & Co., Philadelphia. Jl 1926.

General botany with special reference to its economic aspects. xvi + 1056 p. *688 f.* P. Blakiston's Son & Co., Philadelphia. S 1926.

[With A. F. Blakeslee] Chromosome and gene mutations in *Datura* following exposure to radium rays. Proc. Nat. Acad. **13**: 75–79. F 1927.

The evolution of plants. *In:* Frances Mason, Creation by evolution, 137–155. The Macmillan Co., New York. 1928.

Gardens within a garden: a general guide to the grounds of the Brooklyn Botanic Garden. Guide No. 2, Brooklyn Bot. Gard. Record **18**: 153–188. My 1929.

Botanic Garden. *Encyclopaedia Britannica* **3**: 942–944. S 1929.

Aeration of tree roots: theory. Proc. Fifth Nat. Shade Tree Conf. 26, 27. F 1930.

The plant world. viii + 136 p. *80 f.* The University Society, Inc., New York. O 1931.

The foundational literature of botany. [Abstract of lecture.] The Teaching Biologist **2**[3]: 1, 4. D 1932.

Plant forms in design. Bull. Metrop. Mus. Art **28**: 126, 127. Reprinted in Brooklyn Bot. Gard. Record **22**: 172–177. Jl 1933.

Adaptations in the plant world. *In:* Frances Mason, The great design, 161–185. The Macmillan Co., New York. 1934.

Effects of radium rays on living cells. Science **82**: 327. 4 O 1935.

The effects of radium rays on plants; a brief résumé of the more important papers from 1901 to 1932. *In:* B. M. Duggar, Biological effects of radiation, **2**: 987–1013. Reprinted as Brooklyn Bot. Gard. Contr. no. 74. 1936.

Botanic gardens of the world; materials for a history. Brooklyn Bot. Gard. Record **26**[3]: 149–353. Jl 1937. ed 2. Brooklyn Bot. Gard. Record **27**: 151–406. N 1938.

Pandemic botany. [Address of the retiring president of the Botanical Society of America, given at Indianapolis, 29 D 1937.] Science **87**: 285–292. 1 Ap 1938.

[With A. H. Graves and M. Free] The herb garden at the Brooklyn Botanic Garden. Brooklyn Bot. Gard. Leafl. **25**[2–4]: 1–12. S 1938.

Gardens within a garden: a general guide to the grounds of the Brooklyn Botanic Garden. ed. 2. Brooklyn Bot. Gard. Record **29**: 157–213. *21 f.* Jl 1940.

Popular and scientific horticulture in a botanic garden. [Address delivered before the American Institute of Park Executives, Cleveland, Ohio, 25 S 1940.] Parks & Recr. **24**: 167–173. D 1940.

The Raphael of flowers. [Text for "Les Roses"; folio of 12 reproductions, in color, of plates by Pierre-Joseph Redouté.] Am. Engraving Co., New York. S 1941.

Theatres, gardens, and horticulture. [Address in acceptance of the 1941 Arthur Hoyt Scott Horticultural award and in dedication of the new open-air theatre at Swarthmore College.] Science **95**: 635–639. Je 1942.

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BREEDING NEUROSPORA FROM ABORTED ASCI

B. O. DODGE AND ANITA APPEL

When one would like to conduct breeding experiments with haploid races of *Neurospora* both of which carry the recessive lethal "*d*" for ascus abortion, the limiting factor would appear to be that no ascospores are formed in the F_1 (*dd*), asci.[1] Therefore, breeding beyond the first generation asci would seem to be out of the question. This paper describes a new method by which, even though every ascus should abort, hybridization studies can yet be carried on generation after generation, without the development of ascospores at any time. It should be clearly understood that we are not referring to results of vegetative propagation as generations, as when one simply transfers cultures or uses conidia or other asexual propagating bodies. We refer, on the contrary, to *new* races obtained through real hybridization, nuclear fusions in the ascus, with subsequent segregation of genetic factors at reduction.

Before we describe our experiments it may be well to recall some of the reasons why an ascus may fail to mature its full complement of ascospores. (1) All eight nuclei may delimit spores, but for some reason certain spores never reach their normal size or mature. For example, when *Neurospora sitophila*, an eight-spored species, is crossed with *Neurospora tetrasperma*, eight spores are cut out in the few asci which one may rarely obtain.[2] In most such asci only three or four of the eight spores ever mature. This is an example of *spore* abortion and not of ascus abortion. (2) In the powdery mildews certain species may very commonly mature only two or three spores in each ascus. This was found by Harper to be due to the fact that after the third nuclear division some of the nuclei become attached to the ascus wall and degenerate without taking any part in spore formation. The two or three nuclei that do not degenerate cut out normal spores. If the failure of an ascus nucleus to perform a normal function of delimiting a spore constitutes an abortion, then we may say that failure to delimit the full complement of ascospores here is due to *nuclear* abortion or nuclear degeneration. In asci homozygous (*Aadd*), for the recessive lethal "*d*" the ascus usually aborts completely (fig. 1, A). It fails altogether to perform its normal function, which is spore formation, for all eight nuclei degenerate. This is *ascus* abortion. (3) Asci heterozygous for the lethal *I* very fre-

[1] **Dodge, B. O.** A recessive factor lethal for ascospore formation in *Neurospora*. Bull. Torrey Club **62**: 117–128. 1935.

[2] ———. Production of fertile hybrids in the ascomycete *Neurospora*. Jour. Agr. Res. **36**: 1–14. 1928.

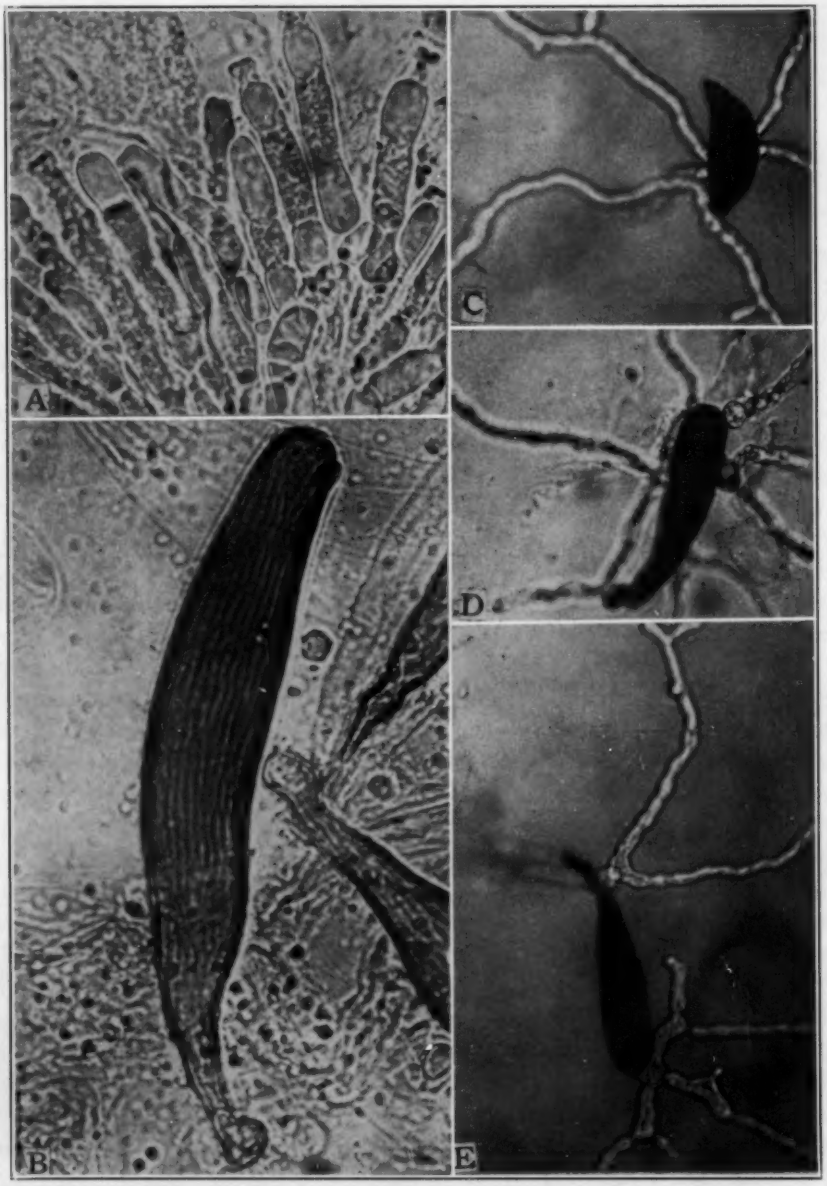

FIG. 1. A, deliquescent ascus abortion of *Neurospora tetrasperma*. All asci were homozygous, *dd*. B, indurated aborted ascus. An effect induced by cultural conditions, and not heritable as such. More highly magnified. C, germination of an abnormal ascospore of the kind rarely developed in asci homozygous for *dd*. Germination here is from a point beneath the spore. D, Growth from or "germination" of an indurated aborted ascus. Note the spherical enlargements from which secondary growth has proceeded. Such enlargements are always present when ascospores germinate. E, same as D except for the location of one of the points from which growth has proceeded. In neither case is there germination by way of the ring-pore at the ascus tip.

quently abort without spore formation.[3] In this case there is a fourth nuclear division which follows very quickly the third division and this upsets the normal course of events so that no spores whatever are formed in such asci (fig. 1, B). These asci with 16 nuclei very often become heavily indurated and take on markings characteristic of the ascospores themselves. In the paper referred to it was indicated that indurated ascus abortion may be due either to heritable genetic factors or to certain cultural environmental conditions. In either case the aborted asci have the same appearance and nuclear behavior is much the same, that is, a fourth nuclear division occurs immediately following the third.

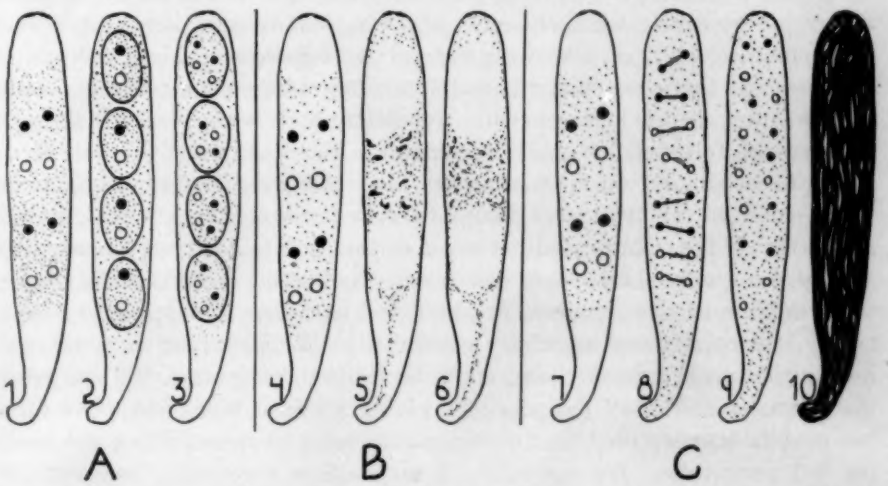

FIG. 2. Diagrams showing nuclear behavior in three types of asci of *Neurospora tetrasperma*. The reduction divisions and the third division which is always equational are not figured. In this respect the picture is the same for all three types. A, in a normal ascus four spores are delimited after the third division, two nuclei of opposite sex being included in each spore. As soon as the spores are fully delimited a fourth division occurs so that there are then sixteen nuclei present in the spore complement of each ascus. B, deliquescent ascus abortion. The eight nuclei move toward the center of the ascus and begin to degenerate. In No. 6 nuclear degeneration is complete. C, indurated ascus abortion. A fourth nuclear division follows very quickly the third division, not allowing time for spore formation. Such asci often become heavily indurated, as shown at C 10 and in Figure 1, B.

Dodge and Seaver[4] described an interesting case where homozygous asci (*dd*), which would ordinarily abort and deliquesce, under certain cultural conditions all became indurated. In other matings many heterozygous asci

[3] **Dodge, B. O.** A lethal for ascus abortion in *Neurospora*. Mycologia **26**: 360–376. 1934.

[4] **Dodge, B. O. & Seaver, Bernice.** The combined effects of the dominant and the recessive lethals for ascus abortion in *Neurospora*. Am. Jour. Bot. **25**: 156–166. 1938.

(*Dd*) for the most part became indurated, while others did delimit some ascospores. Later some of the indurated asci were placed on the surface of agar in Petri dishes under conditions suitable for growth. It was found that hyphal growth seemed to occur from the under side of a few asci, but no growth could be seen from the pore located at the tip end of such as ascus. It was not possible to determine whether or not this growth may have proceeded from conidia which may have been accidentally carried over when the asci were isolated. On other occasions the same experiment was performed with the same results; no positive proof, however, that the indurated ascus actually "germinated" was obtained.

In our recent experiments on heterocaryotic vigor it was very difficult to determine positively whether or not a general heterocaryotic condition had been obtained when certain races were grown together in mixed culture. It was believed that such mixed cultures might produce some ascocarps, even though no general heterocaryotic condition had been reached through anastomoses followed by nuclear migrations. Fertilization could well occur through conidiation or spermatization. In these breeding experiments in which each of the two races mated carried the recessive lethal *d*, it was found that if the culture medium was a certain potato dextrose, homozygous asci (*dd*) not only aborted, but also frequently became indurated. Having in mind the previous experiments in which such asci gave indications of germinating, we carried out carefully controlled experiments for proving definitely that such indurated asci could be made to germinate. We are using this term "germinate" perhaps in a rather strained sense, since the term has usually been applied, in discussing the fungi, to spores which are sending out germ-tubes. We say sclerotia and bulbils germinate, however. Indurated asci are certainly not spores, even though they may have a striately marked wall like that of ascospores.

By growing our races *Ad* and *ad* [5] together on a potato dextrose agar we were able to prevent, in certain cultures, the degeneration of the eight nuclei

[5] *A* and *a* are the sex reaction factors, both of which must be present before an ascus will form. In addition to the recessive, *d*, there will naturally be other factors present; some will be brought along in one race, while the second race in the mating will carry the same or other factors or their alleles. There would be little point in breeding two races which differ only in their sex reaction factors. In the breeding experiments under discussion the fusion nucleus will be homozygous for some factors and heterozygous for others, but we are here concerned with only *A*, *a*, and *d*, factors for sex reaction and factors for homozygous ascus abortion, ignoring for the present the factors involved in heterocaryotic effects. We also assume here that there are 16 nuclei present in an indurated aborted ascus. Sixteen nuclei would result from four divisions, but some of these nuclei may degenerate; or there may be a fifth division, but it would be necessary to have cytological evidence for this statement. Normally, regardless of whether we have an eight-spored ascus like those of *N. crassa*, or a four-spored ascus like those of *N. tetrasperma*, there are in all the spores taken together, 16 nuclei. It is only in the early stages of spore germination that additional nuclear divisions occur.

in some asci, so that a fourth division must have occurred. We assume this is what happened because the aborted asci became indurated. In such asci the 16 nuclei do not degenerate, at least not for some time.

A number of these indurated asci were carefully isolated and placed on the surface of water agar in plates. They were then heated to 58–60° C for one hour. This treatment will kill all conidia which are in contact with a moist surface. It was found that in no case were conidia which survived the heating carried over in the process of isolating the asci. Therefore, whenever hyphal branches appeared to be emerging from beneath or from the side of an indurated ascus we were certain that it was the ascus, not contaminating conidia, that was the source of the growth. There is usually a vesicle or spherical enlargement of the germ tube from which secondary tubes proceed in two or three directions before they branch (fig. 1, D, E). If an indurated ascus can really germinate we should naturally expect the germ-tube to proceed from the pore at the ascus tip.

We do not know the exact cultural conditions which may lead to an indurated ascus abortion which is not heritable. Zickler [6] found that by treating the cultures with chloral hydrate he could induce the formation of giant ascospores which would nevertheless germinate. He figures what he also calls giant spores which completely fill the ascus. These are certainly not spores; they are indurated aborted asci. He does not mention that he obtained outgrowths from such asci. When an ascus contains only a single giant spore, the spore does not completely fill the ascus; there is always some epiplasm left outside the spore. Dodge, in his plate 3, figs. B and F,[7] illustrates very clearly the difference between an ascus with one giant spore, and an indurated ascus.

On the other hand, there are some facts which support the view that an indurated ascus is nothing more than a giant ascospore. (1) The wall of such an ascus is beautifully striated, like that of an ascospore of *Neurospora*. (2) There is a definite ring-pore at the upper end of the ascus. Ascospores have definite germ pores at either end. (3) When an ascus germinates there develops the very characteristic spherical enlargement of the germ-tube soon after it emerges. Such vesicles do not occur when a conidium germinates or when a hyphal cell or fragment sprouts out; they are formed only when ascospores germinate. (4) Heat treatment stimulates indurated ascus germination the same as it does ascospores.

In addition to the reasons given previously in favor of the view that the ascus is a definite morphological unit regardless of how it may function abnormally, it may be said that the striations on ascospores are laid down

[6] **Zickler, H.** Über künstliche erzengung von Miktohaplonten ver Askomyzeten. Biol. Centralb. **51**: 540–546. 1931.

[7] See footnote 2.

from the cytoplasm, no doubt as influenced by genes, now carried in the nuclei of the spore, now carried in the 16 nuclei distributed in the cytoplasm of the indurated ascus. All asci of *Neurospora* have an elastic ring-pore at the apex. This is a mechanism which has a function in the violent discharge of the ascospores.

Cultures obtained from indurated asci which were homozygous *dd* gave perithecia with asci which in turn, especially on corn meal agar, showed the deliquescent type of abortion. This proved that the factors *A*, *a* for sex reaction, as well as the recessive lethal *d* factor had been passed on to the f_1 races, now heterocaryotic because they had arisen through outgrowths from a heterocaryotic ascus. We have attempted to induce the deliquescing type of aborted asci to "germinate," but as yet with no success. Theoretically they could not do this because their eight nuclei have already gone through the first stages of degeneration. The sixteen nuclei in an indurated ascus persist for some time.

As noted in a previous paper [8] such an ascus does occasionally delimit a few abnormal spores on spore-like bodies. Some asci from our recent matings of new races, each carrying the lethal *d*, at times did cut out rather abnormal-looking spores. We have found that some of them can be germinated (fig. 1, C). Cultures from such ascospores usually produced ascocarps, which always had aborted asci. Such ascospores would be perfectly satisfactory for analyzing the genetic factors represented in an ascus, provided one obtained three or four bisexual spores from the same ascus. It is believed, however, that one could more certainly obtain all the inheritance or component nuclei resulting from reduction by working with an indurated ascus. In either case the final step in continuing the breeding experiment would be to separate out the individual component f_1 races either by plating out conidia or microconidia, or by isolating single hyphal tips.

The senior author some years ago, while working with cultures of *Pezizella Lythri*, found that one could obtain "germination" or growth from the penultimate cell of the ascus crosier. Where this occurred one could see plainly that the young ascus was just beginning to develop. Since nuclear fusion occurs very early, or before the ascus elongates to any extent, it may be that we were seeing germination of a cell which was still diploid! Or it may be that reduction was occurring at germination, a sort of reversion to a primitive type in which the zygote reduces at germination. More likely, however, nuclear fusion had not yet taken place. Miss Angie Beckwith, who undertook to continue this work, later reported personally that she obtained what seemed to be perfectly normal mycelia from such proliferating ascus cells or primordia, and that normal conidia were later developed in her cultures.[9]

[8] See footnote 1.

[9] Unpublished work.

The particular importance of this kind of germination is that it results in the production of heterocaryotic mycelia. We find in recent literature the statement that a dicaryotic cell of a rust or of a mushroom is in fact diploid because the genes carried in each of its two haploid nuclei operate just as they would if they were included in the same nuclear membrane. The authors of such statements should realize that when the two haploid nuclei of a rust dicaryon fuse, so that all their genes are included within the same membrane, a mature teliospore results. When the two haploid nuclei in the mushroom dicaryon fuse so that their complementary genes are now within the same membrane, a basidium is formed. So it is clear that the manifestations of genes carried in the haploid nuclei of a dicaryon cannot possibly be the same as they are when drawn together within the same membrane of a diploid nucleus. What we should emphasize and insist on is that when the vegetative structure of a fungus contains two or more kinds of haploid nuclei, the effect, physiologically and morphologically, is the resultant of the combined, or the complementary, effects of all the genes working in the same cytoplasm. Complementary genes may be located in the same haploid nuclus or in two different haploid nuclei in the same cytoplasm. In such case we can say without fear of contradiction that it does not make any difference whether these genes are in the same nuclear membrane or not,[10] so long as we do not bring them together through a nuclear fusion. This is quite different from saying that a dicaryotic cell, because it contains two haploid nuclei, is diploid, and that it can be heterozygous or homozygous as the case may be. It is still a dicaryotic cell, and it can be heterocaryotic or homocaryotic as the case may be.

It remains to discover just what cultural conditions result in indurated ascus abortion, without the intervention of the dominant lethal *I*. Some such method as that described by Zickler would be effective; or it may be that high temperatures during certain critical stages in the development of the asci would yield the same result. This is a problem requiring a more extensive study, but it will be worth while if one wishes to pursue either morphological, physiological, or genetical studies on heterocaryotic structures of *Neurospora*.

SUMMARY

Asci of types of *Neurospora tetrasperma* homozygous for *dd* abort and usually deliquesce without ascospore formation. This fact prevents breeding beyond the first (F_1) asci if both parents in the matings carry this recessive lethal, *d*. Deliquescent ascus abortion is due to the degeneration of the eight nuclei without spore delimitation. Certain cultural or other environ-

[10] **Dodge, B. O.** Heterocaryotic Vigor in *Neurospora*. Bull. Torrey Club **69**: 75–91. 1942. Reports from Recipients of Grants from the Research Funds. Year Book Am. Phil. Soc. 148–150. 1942.

mental conditions may, however, prevent nuclear degeneration, with the further result that a fourth division occurs. The ascus with 16 nuclei is marked by a thickened, brown, and striated ascus wall. Such asci resemble somewhat giant ascospores. When they are heated to 60° C for one hour, many of them will germinate. A way is thus provided for breeding generation after generation with the recovery of all the different types of nuclei coming from each mating even though the asci regularly abort. Occasionally in certain races a homozygous ascus (*dd*) does cut out one or two abnormal spores. Such spores can also be germinated, but one is not sure of recovering all four possible types of nuclei from an ascus.

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STUDIES IN DREPANOCLADUS—I.[1]

History, Morphology, Phylogeny, and Variation

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HISTORICAL ACCOUNT OF THE GENUS

Although the name *Drepanocladus* was not proposed until 1851, several of the species included were described under *Hypnum* by Hedwig and previous workers. It is therefore necessary to trace the concept of the genus *Drepanocladus* from the beginning of bryological nomenclature.

In his fundamental work, *Species Muscorum,* Hedwig (1801), included only three of the species now placed in *Drepanocladus—Hypnum aduncum, H. fluitans* and *H. uncinatum.* Turner (1804) in his *Spicilegium* considered these three and added *Hypnum revolvens.* Bridel (1812), in the second supplement of *Muscologia Recentiorum,* added *Hypnum lycopodioides.*

As early as 1827 the species of *Hypnum* with unicostate, falcate-secund leaves were recognized as a unit and, in this *Bryologia Universa,* Bridel (1827) segregated them under the heading, which may be interpreted as a section, "Adunci." In this work he placed 65 of the species of *Hypnum* in the subgenus *Stereodon;* 8 of these are included under "Adunci." He does not state that *Stereodon* is a subgenus but it is not numbered in the series with the genera so cannot be considered a genus. That he was familiar with the concept of the subgenus is evidenced by the statement in the preface: "Sic genus *Campylopus* melius instituimus, speciebus omnibus quae calyptra mitriformi utuntur ab illo detractis et in genus novum nobis *Dryptodon* dictum quodque *Grimmiam* tanquam subgenus continuat, conflatis." The species included under "Adunci" are *Hypnum Stereodon aduncus, fluitans, uncinatus, lycopodioides,* and *scorpioides* with three other species still in *Hypnum* and one species now in *Hylocomium.*

In his *Synopsis Muscorum,* Müller (1851) further segregated these species into section *Mallacodium* and created the name *Drepanocladus* for the subsection which included *H. riparium* (now in *Leptodictyum*), *H. uncinatum, H. fluitans, H. aduncum, H. revolvens,* and *H. paradoxum.*

The first monographic treatment of the present species of *Drepanocladus* appeared in the *Bryologia Europaea* (1854, 1866) where the group was treated as Section VII of *Hypnum* under the descriptive heading: "Caulis erectus vel prostratus, folia falcato-secunda, unicostata." To the species earlier considered were added *H. exannulatum* in the monograph and *H.*

[1] This is the first of a series of four articles on *Drepanocladus;* the others will appear in BRITTONIA, THE AMERICAN MIDLAND NATURALIST, and THE BRYOLOGIST.

Cossoni, *H. Sendtneri*, and *H. vernicosum* (described first in 1861 by Lindberg) in the first supplement. Our present species *Drepanocladus Kneiffii* appeared first in the *Bryologia Europaea* under the genus *Amblystegium*. All the species are described with the completeness and accuracy and illustrated with the beauty characteristic of the *Bryologia Europaea*.

Bridel's recognition of the group "Aduncí" was followed by subsequent workers in *Hypnum*. In *The Musci and Hepaticae of the United States* Sullivant (1856) proposed the subgenus *Harpidium* to include essentially the same species, namely, *Hypnum aduncum*, *H. uncinatum*, *H. revolvens*, and *H. fluitans*. Schimper, in his two editions of *Synopsis Muscorum Europaeorum* (1860, 1876) placed in the subgenus *Harpidium Hypnum Kneiffii*, *H. aduncum*, *H. lycopodioides*, *H. exannulatum*, *H. fluitans*, *H. revolvens*, *H. uncinatum* (in ed. 1), and *H. vernicosum*, *H. Cossoni*, *H. Sendtneri*, *H. hamifolium*, *H. pseudostramineum*, and *H. Molendoanum* (in ed. 2).

De Notaris (1838) in his *Syllabus Muscorum* included *H. scorpioides*, *H. lycopodioides*, *H. aduncum*, *H. fluitans*, and *H. uncinatum* with several other species of *Hypnum* in Section "Aduncа" of *Hypnum*. However in his *Bryologia Italiana* (1869) he transferred the following species to *Amblystegium* II *Macrophylla* (which included also several present species of *Amblystegium* and *Hypnum*): *H. Rotae*, *H. lycopodioides*, *H. Sendtneri*, *H. revolvens*, *H. fluitans*, *H. uncinatum*, *H. exannulatum*, and *H. Kneiffii*.

Hartman and Lindberg, in Hartman's *Skandinaviens Flora* (ed. 5, 1849; ed 8, 1861; and ed. 9, 1864) proposed the new species *Hypnum badium*, *H. vernicosum*, and *H. intermedium* but did not add, in their floristic treatments, anything new to the concept of the group as a whole.

By 1869 the concept of the genus *Drepanocladus* as we know it today was well defined and most of our present species had been described. The process until this time had been to describe the species and to group them according to their relationships. Beginning in 1880 with Sanio's work a tendency developed to split this small group of species into many species, subspecies, varieties, and forms. The present genus *Drepanocladus* was shifted from *Amblystegium* to *Hypnum* and back again several times during this period.

Carl Sanio, in numerous papers from 1880–1887, treated the group as the subgenus *Harpidium* of *Hypnum*.[2] His classification, following a

[2] Commentatio de *Harpidiis* europaeis indirectiva. Bot. Centralbl. 1880 (Beilage 2): 1–24. 1880. Additamentum in *Hypni aduncí* cognitionem. Bot. Centralbl. **5**(3): 93–95. 1881. Additamentum secundum in *Harpidiorum* cognitionem. Bot. Centralbl. **13**(13): 425–440. 1883. Beschriebung der Harpidien, welche vornehmlich von Dr. Arnell während der Schwedischen Expedition nach Sibieien im Jahre 1876 gesammelt wurden. Sv. Vet.-Akad. Handl. **10**(1): 1–62. 1885. Bryologische Fragmente. Hedwigia **26**: 99–109; 129–169; 194–214. 1887.

typographically complicated system of Greek and Roman letters and numerals, indentations, asterisks, and daggers, is obscure and difficult to interpret. He described many new species, varieties, and forms, and gave formal recognition to every possible minor habitat variation. Although some of his descriptions are long and detailed, others are extremely meager and all are without definite measurements of any kind. Fortunately, most of his names have never been used for American plants, and so they need not be included in the synonymy here.

Boulay's treatment of Section *Harpidium* of *Hypnum* in *Muscinées de la France* (1884) was original and complete and the best monographic treatment of the group since the *Bryologia Europaea*. He collected the many scattered references to numerous species which had been proposed in the journals and pamphlets between 1866 and 1884 and put the material into workable form. His work is good because of its full detailed descriptions, excellent habitat notes, and comments on diagnostic features and relationships. With each revision of the group, more varieties appeared, and Boulay, no exception, proposed numerous new ones to add to the already long list.

Renauld's greatest contribution to the concept of the genus *Drepanocladus* was his indication of a variety or forma "typicum" for *Hypnum aduncum*, *H. fluitans*, and *H. revolvens*. Previously, no one had ever indicated the concept of a "typical" plant, which was rapidly being lost in the maze of varieties. I think it is safe to say that the modern concept of the genus begins with Renauld's work. His revision of Section *Harpidium* of *Hypnum* in Husnot's *Muscologia Gallica* (1894), supplemented by his numerous smaller papers,[3] is extremely useful, as much for its notes of habit and relationships and its illustrations as for its taxonomic revision. His use of the ambiguous category "groupe" and "sous-groupe" often makes his nomenclature and classification obscure. Renauld retained many of Sanio's and Boulay's names and created many new, inadequately described varieties and forms.

Between 1875 and 1918 numerous local floras included treatments of the present genus *Drepanocladus*. In Berggren's *Musci et Hepaticae Spetsbergenses* (1875) several new varieties were proposed for these species, which he included under *Hypnum*. Lange and Jensen (1887) in their treatment of *Harpidium* in *Conspectus Florae Grønlandicae* gave full generic recognition to what had previously been a subdivision of *Hypnum*. The group, with new species, was included with *Amblystegium* by Lindberg and Arnell (1890) in *Musci Asiae Borealis* and Arnell and Jensen (1907) in *Die Moose des Sarekgebietes*. However, Bryhn (1906) in reporting the bryophytes of

[3] Classification systématique de la section *Harpidium* du genre *Hypnum* de la flore française. Rev. Bry. **8**: 73–82. 1881. Causerie sur les *Harpidia*. Rev. Bry. **33**: 89–100. 1906; **34**: 7–14. 1907. Notes sur quelques *Drepanocladus*. Rev. Bry. **36**: 129–138. 1909; **37**: 29–34. 1910.

the second expedition of the "Fram" and Hesselbo (1918), in *The Bryophyta of Iceland*, both considered the species in *Hypnum*.

The American publications of this period (Lesquereux and James' *Manual of the Mosses of North America* (1884) and Kindberg in Macoun's *Catalogue of Canadian Plants* (1892)) treated the group as the subgenus *Harpidium* of *Hypnum*.

Limpricht (1897–1898) in *Die Laubmoose Deutschlands, Oesterreichs, und der Schweiz*, includes 19 species in *Hypnum*, subgenus *Drepanocladus*, with full descriptions and measurements, and detailed distribution notes. Although every species is not illustrated, the pictures provided are clear and helpful.

Although Müller is responsible for the name *Drepanocladus*, Warnstorf, in his article "Die Europäischen Harpidien" was the first to use it as a genus and make the combinations.[4] His article is important because of its comprehensive treatment which includes many new combinations as well as a historical survey of the literature, a general discussion of the relationships of the species, a key to the species, descriptions, and the distribution. Warnstorf (1906) followed his excellent and useful monograph with an equally fine treatment of *Drepanocladus* in *Kryptogamenflora der Mark Brandenburg*. His keys and descriptions are complete and detailed but of his 24 species, only 7 can be recognized as valid species; the remainder of his names have been reduced to either varieties or symonyms. Not only did he divide the genus into many species, but also he included innumerable varieties for each species. He, like Boulay, Renauld, and Limpricht, was a "splitter."

Roth (1905) in *Die Europäischen Laubmoose* treats 22 species of *Drepanocladus* with full descriptions, citations, and references. His treatment resembles Warnstorf's in that over half of his species are today recognized as merely varieties or habitat phases.

Loeske[5] in an article "Drepanocladus, eine biologische Mischgattung" discussed the morphology of the group and its relationship to closely related genera and proposed the following names as genera. Although he indicated the species to be included, his new genera are *nomina nuda*, since he gave no descriptions of them.

1. *Sanionia—uncinata, orthothecioides, contigua.*
2. *Limprichtia—vernicosa, intermedia, revolvens.*
3. *Warnstorfia—exannulata, orthophylla, tundrae, purpurascens, fluitans* and varieties.
4. *Drepanocladus—aduncus* and varieties.
5. *Pseudocalliergon—turgescens, trifarium, longicuspis.*
6. *Scorpidium—scorpidioides.*

[4] Beih. Bot. Centralbl. **13**: 338–430. 1903.

[5] Hedwigia **46**: 300–321. 1907.

In his *Studien zur vergleichenden Morphologie und phylogenetischen Systematik der Laubmoose* (1910) he discusses these groups in more detail and supplements his statements of relationships among the species in the group. However, his names are still without generic descriptions.

Mönkemeyer's treatments of *Drepanocladus* in Pascher's *Süsswasser-Flora* (1914, 1931) and in *Die Laubmoose Europas* (1927) initiated the present tendency to reduce the number of species in the genus. There is no essential difference among his three publications; each includes the same eight species with keys, illustrations, and descriptions. Although he decreased the number of species, he included a large number of varieties and forms under each.

Brotherus, in "Die Laubmoose Fennoskandias" (1923) and in *Die natürlichen Pflanzenfamilien* (1925) adopted Mönkemeyer's policy of reducing the number of species and followed in large part his arrangement of varieties and forms. He used Loeske's proposed genera as sections and added section *Pseudo-Drepanocladus* for *Hypnum badium* Hartman.

Although writing as late as 1924, in *The Student's Handbook of British Mosses,* Dixon still included the species of *Drepanocladus* in *Hypnum,* subgenus *Harpidium.* His treatment follows Renauld's monograph with slight differences. The comments on distinguishing features, inter-specific and inter-varietal relationships, and habitats are his most valuable contribution.

The most recent treatment of *Drepanocladus* is Grout's in *Moss Flora of North America* (1931). As he states in his introduction, he has based his work on Renauld's and Mönkemeyer's published monographs and on their identified specimens.

As has been seen from the preceding synopsis, the concept of the genus *Drepanocladus* developed in Europe and most of the type localities are European. Because most of the species were described before the type concept was developed, types have never been designated. Under present world conditions it has been impossible to borrow material from Europe. However, the concept of the species has been so well developed in European and American literature and American herbaria that it has been possible to interpret American material from the descriptions, illustrations, and specimens. Because of the impossibility of studying European types and herbarium material, I have been forced to confine the scope of this monograph to North America. Therefore, only American material and names have been included; names which have never been used for American plants have not been considered.

MORPHOLOGY

Habit. The variability of *Drepanocladus* in habit, branching, and size depends largely on habitat conditions. *Drepanocladus uncinatus,* which most

frequently creeps over the ground, logs, or rocks, is irregularly or regularly pinnately branched. The stems of *D. aduncus* when growing among grass or reeds in swamps and marshes are creeping and fastigiately or irregularly pinnately branched. Submerged, floating stems are usually long, but may be either simple or regularly pinnately branched. Large, plumose fronds result when the stems are pinnate in the aquatic phase of *D. aduncus*, *D. fluitans*, or *D. exannulatus*. *D. uncinatus* var. *subjulaceus*, *D. exannulatus*, *D. brevifolius*, and *D. badius* often grow 5–8 cm. high, their stems erect, and simple or fastigiately branched. In bogs, *D. vernicosus*, *D. revolvens*, *D. aduncus*, *D. fluitans*, and *D. exannulatus* grow suberect in tufts and are fastigiately or irregularly pinnately branched. Sudden changes in environmental conditions may produce several long branch innovations near the tips of the stems.

Color. Although color is variable in *Drepanocladus*, it is reasonably characteristic for each species. *D. uncinatus* is from shining golden to yellow-green; *D. vernicosus* is light yellow-green; *D. aduncus* is from yellow-green to grass-green; *D. fluitans* is from dull yellow-green to brown; *D. exannulatus* is from crimson to red or purple; *D. revolvens* is from green to deep red or black and has a metallic sheen; *D. brevifolius*, *D. badius*, and *D. lycopodioides* are deep golden at the growing tips and brown or black below.

Stems. The apical buds of stems and branches are always pointed and are usually falcate-secund (except in *D. aduncus* var. *Kneiffii* and depauperate forms of *D. exannulatus*). However, in *Drepanocladus*, the apical buds are never cuspidate as is characteristic in the closely related genus, *Calliergon*.

The stems of *Drepanocladus* generally lack paraphyllia and radicles. Pseudoparaphyllia are produced in the axils of the branches of *D. uncinatus*. Some plants of *D. fluitans* and *D. badius* produce radicles from the apex, base, margin, or costa of the leaves.

The stems of all the species of *Drepanocladus* (except *D. vernicosus* in which the central strand is lacking) show in cross section a small central strand of 3–6 cells embedded in a loose ground tissue. The 2–3 rows of cortical cells may or may not be incrassate or colored. The outer layer of cortical cells of *D. revolvens* is enlarged. Stems vary in diameter from 2–6 mm.

Leaves. Although the leaves of *Drepanocladus* are typically falcate, and may further be strongly and regularly circinate (*D. uncinatus* and *D. revolvens*), they are straight in *D. aduncus* var. *Kneiffii* and the short-celled environmental phases of *D. fluitans* and *D. exannulatus*. In submerged

plants the curvature of the leaves is decreased and the acuminations are long, lax, and twisted. The strongly falcate leaves of *D. aduncus, D. fluitans,* and *D. exannulatus* are channelled at the apex, whereas the straight leaves of some of their varieties have a flat apex.

The leaves of *Drepanocladus* range from strongly and regularly plicate, through irregularly plicate and striate, to completely plane. *D. uncinatus* is the only species of the genus with strongly regularly plicate leaves; the plications are distinctive because each fold extends continuously from the base of the leaf to the apex. The leaves of *D. vernicosus* are plicate only in the broadened basal part, with the apex flat. Forms of other species (*D. exannulatus, D. fluitans,* and *D. aduncus*) may become irregularly striate or sulcate in response to certain environmental conditions. This and similar characters, resulting from habitat conditions, are usually not constant on any plant. In the other species, *D. revolvens, D. lycopodioides, D. badius,* and *D. brevifolius,* the leaves are not folded in any way; they are plane or concave.

The shape of the leaves of *Drepanocladus* varies from broadly oval to linear-lanceolate. Leaves of small plants of *D. aduncus* are broadly ovate; leaves of *D. aduncus* var. *Kneiffii, D. badius, D. lycopodioides, D. brevifolius, D. fluitans,* and *D. exannulatus* are broadly lanceolate; leaves of *D. exannulatus* and aquatic plants of *D. aduncus* are long lanceolate; leaves of aquatic plants of *D. fluitans* are linear-lanceolate.

The acumination may be short and abrupt or long and gradual. Half the length of the leaf of *D. uncinatus* is the long, subulate acumen. The acumination of *D. vernicosus* is abrupt and broad. The leaf of *D. revolvens* is gradually narrowed until within 0.3–0.5 mm. of the apex where it is rapidly narrowed to a filiform point. Forms with ovate or broadly lanceolate leaves are usually abruptly short-acuminate whereas forms with long-lanceolate or linear-lanceolate leaves are gradually long-acuminate. In general, long leaves with long acuminations are produced by complete submergence.

The leaves of all the species of *Drepanocladus* clasp the stem, and are erect rather than spreading. The alar region of the leaf may or may not be decurrent. As a result of variation in decurrency, the line of insertion of the leaf varies from truncate, through broadly or narrowly concave to circular. The alar cells of *D. aduncus* are decurrent, therefore the base of the leaves is always concave. Whether the line of insertion is widely or narrowly concave depends upon the width of the leaf at the base, the diameter of the stem, and the degree of decurrence of the alar cells. Since the alar cells of *D. fluitans* and *D. exannulatus* are not decurrent, the base of the leaf is truncate. The few quadrate alar cells of *D. uncinatus* are slightly decurrent, thus forming a shallowly concave line of insertion seen when the leaves are

removed from the stem. Leaves of *D. revolvens, D. badius, D. vernicosus, D. brevifolius,* and *D. lycopodioides* with quadrate cells across the entire base are always truncate.

The margin of the leaves of *D. aduncus, D. vernicosus, D. revolvens, D. lycopodioides, D. badius,* and *D. brevifolius* is entire or sinuolate at the base. The leaf margins of *D. exannulatus* and *D. fluitans* are serrulate at the base or apex or both. The long subulate acumination of *D. uncinatus* is distinctly serrulate while the base is entire or only slightly serrulate. Whether the serrulations are distant or close depends upon the length of the cells.

Costa. The leaf costa or nerve of *Drepanocladus* is almost universally single, not forking or double (except in *D. fluitans* var. *Berggrenii*); it varies in length and width. In depauperate forms of *D. aduncus* and *D. fluitans* it is short (1/3–1/4 the length of the leaf) and weak (12–20 μ in diameter at base). In *D. vernicosus, D. uncinatus, D. revolvens, D. exannulatus,* and *D. fluitans* it is long (1/2–5/6 the length of the leaf) and strong (40–80 μ wide at the base). In *D. aduncus* var. *capillifolius* and *D. exannulatus* var. *Rotae* the costa is long-excurrent and 80–150 μ wide at the base, and usually deeply colored. Submerged plants of *D. aduncus* and *D. exannulatus* may develop a wide, deeply colored costa. In all species of *Drepanocladus,* including the varieties with excurrent costa, it is tapering.

The cells of the costa are narrowly linear, and usually longer than the cells of the lamina of the leaf. With the exception of *D. vernicosus,* the costa as seen in cross-section is biconvex with a small central strand. The costa of *D. vernicosus,* like the stem, has no central strand.

Areolation. The leaf cells of *Drepanocladus* are narrowly linear, with the exception of certain habitat phases of *D. aduncus, D. fluitans,* and *D. exannulatus,* in which the median leaf cells are oblong (4–6 μ × 28–32 μ). Cells are longest in *D. fluitans* and *D. exannulatus* (4–6 μ × 60–100 μ) and shorter in *D. aduncus, D. revolvens, D. vernicosus,* and *D. uncinatus.* In general the cells are uniform in size and shape throughout the leaf, being only slighter shorter and broader toward the base in *D. aduncus.*

The cell walls are thin in *D. aduncus, D. fluitans, D. uncinatus* and *D. vernicosus.* In some plants of *D. exannulatus* and *D. aduncus* the walls of basal and alar cells are deeply colored. Basal cells of *D. revolvens* and *D. lycopodioides* are pitted, whereas all cell walls in *D. badius* and *D. brevifolius* are porose. In *D. revolvans* only the basal cell walls are incrassate; in *D. badius* and *D. lycopodioides* all cell walls are incrassate and deeply colored brown or red.

The alar cells of *Drepanocladus* may be large and inflated, small and quadrate, hyaline or colored, thin-walled or incrassate, entire or porose, or any combination of these. In *D. aduncus* the alar cells are inflated and

hyaline, forming distinct auricles extending 1/4–1/3 the distance from the margin to the costa. Only in extremely robust submerged plants are the basal and alar cells colored in *D. aduncus*. In *D. fluitans* the alar cells are slightly inflated and extend 1/4–1/3 the distance from the margin to the costa. The alar cells of *D. exannulatus* are always large, but may be thin-walled or incrassate, hyaline or colored, and form either large triangular groups extending to the costa or a single row of elongated cells across the entire base. The alar cells of *D. badius* are inflated, incrassate, and porose. *D. uncinatus* has a small group of quadrate, hyaline alar cells. The alar cells of *D. vernicosus, D. revolvens, D. lycopodioides,* and *D. brevifolius* are not differentiated at the basal angles, although there are two or more rows of shorter cells (hyaline and thin-walled in *D. vernicosus;* incrassate, porose, and colored in *D. revolvens*) across the entire base of the leaf. In general, if the alar cells are large and inflated they are thin-walled; and if they are incrassate they are smaller.

The incrassate cell walls between any two basal cells of *D. revolvens* are 4 μ thick, usually with 1–3 pits. The two secondary cell walls between two alar cells are 4–8 μ thick in *D. revolvens, D. badius,* and *D. lycopodioides.*

Alar cells differ not only in their size and shape but also in their spatial relationship with the other cells of the leaf. The alar cells of *D. aduncus* and *D. fluitans* intergrade completely with the cells of the lamina of the leaf and the transition is imperceptible. However, in *D. aduncus* the alar cells are ventricose and oriented in a different plane from the other leaf cells so that the alar cells are sharply delimited from the cells of the lamina. The alar cells of *D. exannulatus* and *D. fluitans* are never ventricose nor placed at an angle. *D. exannulatus,* unlike *D. fluitans,* shows an abrupt transition from the alar cells to the cells of the lamina so that the alar region is sharply delimited by the size of the cells.

When leaves of *D. fluitans, D. exannulatus,* and *D. aduncus* are removed from the stems, usually some of the cortical stem cells remain attached to the base of the leaves as long "tails." This does not occur so often in *D. vernicosus, D. uncinatus, D. revolvens, D. badius, D. brevifolius,* or *D. lycopodioides.* One of the differences distinguishing *D. aduncus* from *D. fluitans* and *D. exannulatus* is the transition from the stem cells to the leaf cells; in *D. aduncus* it is gradual, whereas in *D. fluitans* and *D. exannulatus* it is abrupt.

Perichaetium. In all species of *Drepanocladus* the perichaetium sheaths the base of the seta. The outer perichaetial leaves are spreading, from ovate to broad-lanceolate, and either ecostate or with a short costa. The inner perichaetial leaves are costate, long-lanceolate, and from gradually or abruptly acuminate to piliform. The perichaetial leaves of *D. uncinatus,* like the vegetative leaves, are regularly and strongly plicate and serrulate at the

apex. In other species, the perichaetial leaves are smooth or irregularly striate, and entire or serrulate.

Perigonial leaves. The perigonial leaves of all species of *Drepanocladus* are similar. They are ovate, abruptly short-acuminate, with a short costa or ecostate, serrulate or entire.

Sporophyte. The capsule and peristome of *Drepanocladus* are typically Hypnaceous. With the exception of the erect symmetric capsule of *D. uncinatus* var. *symmetricus*, the capsule of all species is asymmetric and curved; it may be plicate or smooth. The exothecial cells are smooth or mamillose. The operculum is rostrate or apiculate, attached in all species (except *D. fluitans* and *D. exannulatus*) by a persistent annulus of 2–3 rows of cells. The peristome is perfect, that is, with sixteen teeth and sixteen segments and alternating cilia. The sixteen teeth are transversely thickened and longitudinally striate. The segments of the inner peristome are longitudinally striate with 2–3 cilia.

PHYLOGENY

Drepanocladus belongs to the subfamily Amblystegieae, which includes all the Hypnaceae which have a single costa and a long arcuate-cylindric capsule.

Generic relationships. *Drepanocladus* is most closely related to *Scorpidium;* in fact, the relationship is so close that they have been grouped together by many bryologists. One species of *Scorpidium* is recognized today—*S. scorpioides.* Milde [6] placed it in the subgenus *Harpidium* with the present species of *Drepanocladus,* and Warnstorf [7] called it *Drepanocladus scorpioides. Scorpidium* has all the characteristics of the genus *Drepanocladus* except that the leaf apex is obtuse or apiculate and the costa is faint, short and double, or lacking. To the naked eye, the two genera are so similar that *Scorpidium scorpioides* resembles a very large *Drepanocladus.*

Although *Calliergon* differs from *Drepanocladus* in its straight leaves and rounded or cucullate apices, the close relationship between the two genera is shown not only in their similarity of areolation and costa, but also by their parallel series of species. The same modifications of alar cells, cell walls, costae, and leaves that separate the species of *Drepanocladus* likewise distinguish the species of *Calliergon.* The two genera occur in the same range and in the same types of habitats and are often found associated.

Calliergidium, intermediate between *Drepanocladus* and *Calliergon,* seems to be an artificial genus. One of its species, *C. pseudostramineum,* is

[6] Bryologia silesiaca. p. 350. 1869.

[7] Kryptogamen-Flora der Mark Brandenburg und angrenzender Gibiete. 2: 1027. 1906.

so closely related to *Drepanocladus* that Warnstorf [8] and Brotherus [9] have considered it a form of *D. fluitans*. Grout [10] has considered the erect and straight leaves with blunt apices sufficiently distinctive to separate *C. pseudostramineum* from *Drepanocladus*. In general habit, the plants named *D. pseudostramineum* I have seen have resembled *Calliergon* more than *Drepanocladus*. Further collections of these two species, will, I believe, dispense with this artificial genus and place its species in *Drepanocladus* and *Calliergon*.

In a phylogenetic arrangement, *Drepanocladus* and *Calliergon* form a related species-complex to which the other members of the subfamily are less closely allied.

The species of *Hygrohypnum* with falcate, acuminate leaves and a single costa superficially resemble the species of *Drepanocladus*. However, the species with straight, blunt leaves and short, double costae are never confused with *Drepanocladus*. Furthermore, *Hygrohypnum, Hygroamblystegium,* and *Leptodictyum* grow most frequently in running water, whereas *Drepanocladus* occurs usually in still water. *Hygrohypnum* is so variable and heterogeneous a group that it is difficult to determine its relationship to other genera.

Cratoneuron, in spite of its falcate leaves, decurrent alar cells, and single costa, is distinctive from *Drepanocladus* because of its numerous paraphyllia. It is the only genus in the subfamily which has developed paraphyllia and it therefore holds a unique place in the phylogeny of the Amblystegieae.

Hygroamblystegium is separated primarily from *Amblystegium* on the basis of its aquatic habitat. On the same basis it is more closely allied to and more often confused with *Drepanocladus* than is *Amblystegium*. However, any similarity between *Hygroamblystegium* and *Drepanocladus* is only superficial, for the robust habit, erect-spreading, non-falcate leaves, and thick-walled rhomboidal leaf cells distinguish *Hygroamblystegium*.

Leptodictyum, like *Hygroamblystegium,* resembles *Drepanocladus* only superficially in its aquatic habitat. The leaves are never falcate, but are always erect or erect-spreading, and the alar cells are never inflated. These characters distinguish species of *Leptodictyum* from *Drepanocladus aduncus* var. *Kneiffii,* the only *Drepanocladus* to which it shows any similarity.

Plants of *Amblystegium* or *Campylium* with falcate leaves are sometimes confused with small plants of *Drepanocladus*. *Campylium,* with its typically squarrose-recurved, broadly ovate or lanceolate leaves, is unlike any species or variety of *Drepanocladus*. *Amblystegium* is distinct in its short leaf cells, erect-spreading leaves, and quadrate or only slightly inflated alar cells.

[8] L.c., p. 1040.

[9] Die Laubmoose Fennoskandias **1**: 479. 1923.

[10] Moss flora of North America north of Mexico **3**(2): 100. 1931.

Interspecific relationships. The origin of the species of any group is a speculative but nevertheless an interesting and significant problem. From the comparative morphology of the species of *Drepanocladus*, it is possible to deduce the relationships and to postulate the origin of the species of the genus.

Two general trends of development in the genus have been (1) the production of inflated cells, and (2) the production of alar cells which are not inflated, but which may be differentiated in other ways (see figure 1).

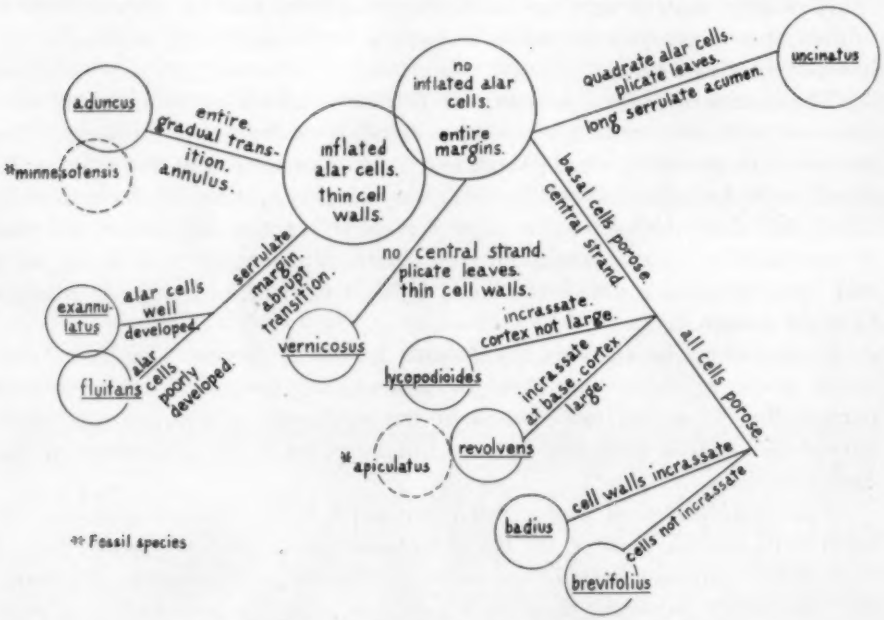

FIG. 1. Inter-relationships of the species of *Drepanocladus*.

Drepanocladus aduncus, *D. fluitans*, and *D. exannulatus* have inflated alar cells and are obviously closely related. An early ancestor must have furnished to all three species the inflated alar cells, and thin cell walls which are not pitted. Subsequent segregation of traits gave rise to (1) *D. aduncus* with entire margins and a gradual transition from the cortical stem cells to the leaf cells, and to (2) *D. fluitans* and *D. exannulatus* with serrulate margins and an abrupt transition from cells of the stem to the cells of the leaf, and the annulus lacking on the capsule. Further evolution has segregated *D. fluitans* with its delicate habit and its poorly developed alar cells which intergrade completely with the cells of the lamina, and *D. exannulatus* with its robust habit and its well developed, clearly delimited alar cells extending across the entire base of the leaf.

Development of the three species, *D. fluitans*, *D. exannulatus*, and *D. aduncus* must have been parallel, because the series of varieties in each is

similar. These three species respond to the same environmental conditions with the same modifications. Each species when growing submerged produces longer stems, longer leaves at greater intervals on the stems, longer leaf cells, and regular pinnate branching. Each species also produces a short-celled, short-leaved phase when it grows in certain unfavorable conditions. Although the variety with an excurrent costa is lacking in *D. fluitans,* it is present in both *D. aduncus* (var. *capillifolius*) and *D. exannulatus* (var. *Rotae*). *D. aduncus,* unlike *D. fluitans* and *D. exannulatus,* produces a variety with straight leaves (var. *Kneiffii*).

The other evolutionary trend, the production of alar cells which are not inflated, gave rise by various combinations of characters to the other species of the genus. Any postulation of the order in which these forms were produced would be pure speculation. *D. vernicosus, D. revolvens, D. brevifolius,* and *D. lycopodioides* are similar in the absence of any differentiated cells at the basal angles of the leaf, and in the presence of several rows of differentiated cells across the entire leaf base. *D. vernicosus,* the only species in the genus without a central strand, is distinct in its stem structure, and in its characteristically plicate and abruptly acuminate leaves with thin-walled cells.

Drepanocladus revolvens and *D. lycopodioides* may have developed from the same stock. *D. revolvens* has only the basal cells incrassate and pitted, whereas, in *D. lycopodioides,* all the cell walls are incrassate with the basal cell walls very thick and porose. The tendency toward incrassate, porose cell walls, partially developed in *D. revolvens,* is intensified in *D. lycopodioides.* The two species differ slightly in stem structure; the outer layer of cortical cells in *D. revolvens* is enlarged, whereas all the cortical cells are of the same size in *D. lycopodioides.* In habit and leaf shape the two species are similar except that *D. lycopodioides* is larger and more robust than *D. revolvens.*

Drepanocladus brevifolius and *D. badius* developed the same cell-wall modifications to produce plants in which all the leaf cells are porose. In *D. brevifolius* the cell walls are uniform in thickness and not, or only slightly, incrassate, whereas in *D. badius* all cell walls are incrassate with the basal cells especially strongly thickened. There are minor differences between the two species in the alar cells: in *D. brevifolius* there are no differentiated alar cells, but some leaves have a row of slightly inflated cells across the insertion of the leaf; *D. badius* always has some differentiated cells, either at the basal angles or across the entire base of the leaf.

Drepanocladus uncinatus is so distinct from all the other species of the genus that it seems probable that it developed along a separate line from the other members of the group. It has neither the inflated alar cells of *D. aduncus, D. fluitans,* or *D. exannulatus,* nor has it the basal row of dif-

ferentiated cells characteristic of *D. vernicosus, D. revolvens,* and *D. lycopodioides.* Instead, a group of quadrate alar cells is always present. The regular, long plications and the long, subulate, serrulate acumen are characteristic of *D. uncinatus.* Not only is *D. uncinatus* distinctive in its diagnostic features, but also in its habitat. It is the only species of *Drepanocladus* which is xerophytic or mesophytic rather than hydrophytic. In fact, *D. uncinatus* is so distinct that Loeske created the genus *Sanionia* for *D. uncinatus* and its varieties (see above).

From *D. uncinatus* developed the var. *symmetricus* with erect symmetric capsules but otherwise with the gametophytic characters of the species; this variety is restricted in its range to the western part of North and South America.

VARIATION IN DREPANOCLADUS

The species of *Drepanocladus* are well defined and have been known for a long time. On the other hand, the many forms and varieties which have been proposed for some of the species have been poorly defined and troublesome for taxonomists. I believe that lack of understanding of the variation in the genus is responsible for the taxonomic dilemma which confronts bryologists working in it.

Variation is of two sorts: that which is initiated by environment and that which is based on heredity. Botanists have confused these two types of variation in many groups of plants, including *Drepanocladus.*

American bryologists have recognized that species of *Drepanocladus* respond to changes in environment to a startling degree. Grout [11] states: "In 1929, in a pond not far from Cold Spring Harbor, was collected *Drepanocladus fluitans gracilis.* In 1931, when the water was low, there was a vigorous emergent growth, the upper leaves of which were typical *D. fluitans Jeanbernati,* while the lower leaves, grown apparently while submerged, were those of var. *gracilis.* On some of the shoots were leaves nearly typical of *D. fluitans* proper. This seems to show that in *Drepanocladus,* at least, habitat conditions modify structure profoundly." Conard[12] investigated the same pond in 1933 and 1934 and found the same conditions to exist: "In wet seasons this moss is the var. *gracilis,* but in dry seasons it becomes var. *Jeanbernati.*" I have not recognized these two so-called varieties, *Jeanbernati* and *gracilis,* because they, along with many others, are merely environmental fluctuations.

Sporophyte characters are of little value in determining species of *Drepanocladus.* With the exception of *D. fluitans* and *D. exannulatus* which have no annulus on the capsule, and *D. uncinatus* var. *symmetricus* which

[11] Miscellaneous notes on mosses. Bryologist **36**: 25, 26. 1933.

[12] The plant associations of Central Long Island—A study in descriptive plant sociology. Am. Mid. Nat. **16**: 433–516. 1935.

has an erect instead of cernuous capsule, the sporophytes of all species of *Drepanocladus* are identical. Gametophyte characters, therefore, must be used for classification and identification. Great variation in habit, color, branching, leaves, costae, and areolation has led to the publication of many varietal and formal names for extreme plants produced by extreme environmental conditions. Because the most variable species of *Drepanocladus, D. aduncus, D. fluitans,* and *D. exannulatus,* have responded to different environments with similar modifications, a long series of variety and form names have been proposed for each of the species. Most of these subspecific names were first proposed under *Hypnum;* many of them were never transferred to *Drepanocladus.* Submerged plants of *D. aduncus* have been called var. *aquaticum, laxifolium, pseudofluitans,* and *laxum;* of *D. fluitans,* var. *submersum;* of *D. exannulatus,* var. *longifolium.* Small forms of these three species have been given variety and form names such as *gracilescens, tenue, attenuatum, filiforme, brevifolium, tenellum, condensatum,* and *abbreviatum.* Deeply colored plants have been called var. *purpurascens.* Short-celled leaves have been called *polycarpon* and *brachydictyon.* Every possible environmental variation has been named.

When the true nature of variation in *Drepanocladus* is understood, it is possible to eliminate these innumerable varieties which cannot be described nor recognized. The result of such a procedure is that only a few subspecific names remain and these are varieties which are hereditary.

In spite of the fact that bryologists have long recognized that much of the variation in *Drepanocladus* was due to environmental conditions, no attempt has heretofore been made to restrict varieties to hereditary variation. I have given varietal rank only to those variations which appear to be hereditary; environmental fluctuations have been discussed so that they may be recognized as such, but will not be included in the formal taxonomy. When a character is constant in all parts of a plant, regardless of environment, it is apparent that its uniformity is the result of fundamental genetic factors. When a certain character differs on different parts of the same plant—for instance, leaves from different parts of the stem—it is obviously influenced by environmental conditions.

Field and herbarium studies were made to determine which characters were modified by changes in the environment and which remained constant through a changing environment. It was discovered that genetic factors determined (1) whether the costa was excurrent or short and (2) whether the leaves were falcate or straight. Combinations of these two hereditary characters produce three varieties in *D. aduncus:* var. *typicus* with falcate leaves and a short costa; var. *Kneiffii* with straight leaves and a short costa; and var. *capillifolius* with falcate leaves and an excurrent costa. In *D. exannulatus* the leaves are always falcate but the length of the costa varies.

Therefore I have recognized var. *typicus* with a short costa and falcate leaves and var. *Rotae* with an excurrent costa and falcate leaves.

Other characters, such as cell size and leaf length, are influenced by the environment and may vary on the same plant. In *D. aduncus, D. fluitans,* and *D. exannulatus* two habitat phases result from this type of variation: (1) short leaves and broad, oblong-linear cells; and (2) long, flexuose, widely-spaced leaves and long-linear cells. These phases may be found on the same plant, and they may be produced on any of the varieties. Leaves on the lower, and submerged portion of the stem of any of these species may be the aquatic phase (2) while the upper, emergent part of the same stem may be either typical or short-celled (1). However, if the lower, submerged leaves have an excurrent costa, the upper ones will have an excurrent costa also, though the cells may be different. Therefore, since the costa is the constant character, it is apparent that the length of the costa is controlled by genetic factors, while the leaf and cell size are conditioned by environmental factors. Falcate leaves are an expression of hereditary factors, for, if the leaves are falcate in one part of the stem, they will be falcate throughout, even though submerged or subjected to other modifying environmental conditions.

Environmental conditions producing habitat forms in Drepanocladus. The same habitat conditions produce similar forms in *D. fluitans, D. exannulatus,* and *D. aduncus.*

Zastrow [13] carried out controlled experiments on mosses and compared growth submerged and emergent under identical conditions of pH. She found that, in general, growth under water led to pinnate branching, longer leaves, longer leaf cells, larger and more numerous alar cells, widely spaced leaves, and a weaker costa. These modifications are produced by submerged plants of *D. aduncus, D. fluitans,* and *D. exannulatus.*

The short-celled variation often seen in *Drepanocladus* occurs most commonly on the emergent stems of plants growing in water. However, this form appears to be the result of recent flooding. Apparently the form is produced when the plant has more water available than is customary in its habitat. When the water supply is abundant and constant, all the leaves are similar and characteristic of submerged growth. When the water supply fluctuates, different forms are produced on the same plant under the different conditions; one of the forms produced under these conditions is invariably the short-celled phase of *D. aduncus, D. fluitans,* or *D. exannulatus.* Consequently, plants growing in deep lakes are entirely the submerged phase, whereas plants which grow in temporary ponds and pools and intermittent streams produce the short-celled variation on part of their stem.

[13] Experimentelle Studien über die Anpassung von Wasser- und Sumpfmoosen. Pfl.-Forsch. 17: 1–70. 1934.

Field studies around the Huron River, Washtenaw County, Michigan, indicated this type of environmental fluctuation first in 1940. On May 14, when the water level in a pond near the river was high, plants which had produced the short-celled leaves on the emergent stems were collected (*Wynne 1701*). In the summer (June 30) when the pond was stagnant and the water level stable, all the new growth was the aquatic phase (*Wynne 1712*). On August 30 collections again showed that short-celled leaves had been produced by a rise in the water level (*Wynne 2072*). Later (October 15) and until winter the conditions remained stable and all the leaves produced were of the aquatic type (*Wynne 2230*). Similar reactions were observed in Reese's Bog, Cheboygan County, Michigan. June 29, 1942, with much water in the bog, the leaves on the growing stems were short-celled (*Wynne 2453*). With less water (July 30) the plants were producing typical leaves (*Wynne 2591*).

The evidence obtained from these and many similar field observations was substantiated by large herbarium collections and extensive field notes from Quebec by H. Dupret. Many of Dupret's collections are in series from the same locale taken at different dates. When the response of each species to environmental changes was known, then each plant told its own history. By examining leaves from different parts of a stem of *Drepanocladus*, it is possible to tell approximately under what environmental conditions those leaves were produced. This knowledge made possible the interpretation of herbarium specimens and the elimination of environmental fluctuations from the formal nomenclature in the genus.

Statistical studies. In order to understand the variation in the genus *Drepanocladus*, statistical studies, as well as field studies, were made of the variable species. Measurements were made of all diagnostic features including serrulation, acumination, size, attachment, decurrency, and distance apart of the leaves; size of cells at base, alar region, margin, and apex of leaves. By plotting the results, it was easy to see whether the population fell naturally into one or several units. This information was useful in determining whether or not certain varieties were valid.

Figure 2 shows the statistical evidence that was used in determining the varieties in *D. revolvens* and *D. uncinatus*. All collections of *D. uncinatus* were examined and measured and the length of the leaf was plotted on a single histogram. Two populations were then apparent: one with leaves 2.0–4.0 mm. long and another with leaves 4.4–5.5 mm. long. Previous to this study several varieties, called *plumulosum, abbreviatum, plumosum, gracilescens,* and *gracillimum*, had been separated because of shorter leaves and a more delicate habit. When these simple statistical studies indicated that such a separation was artificial, a further, more careful examination of

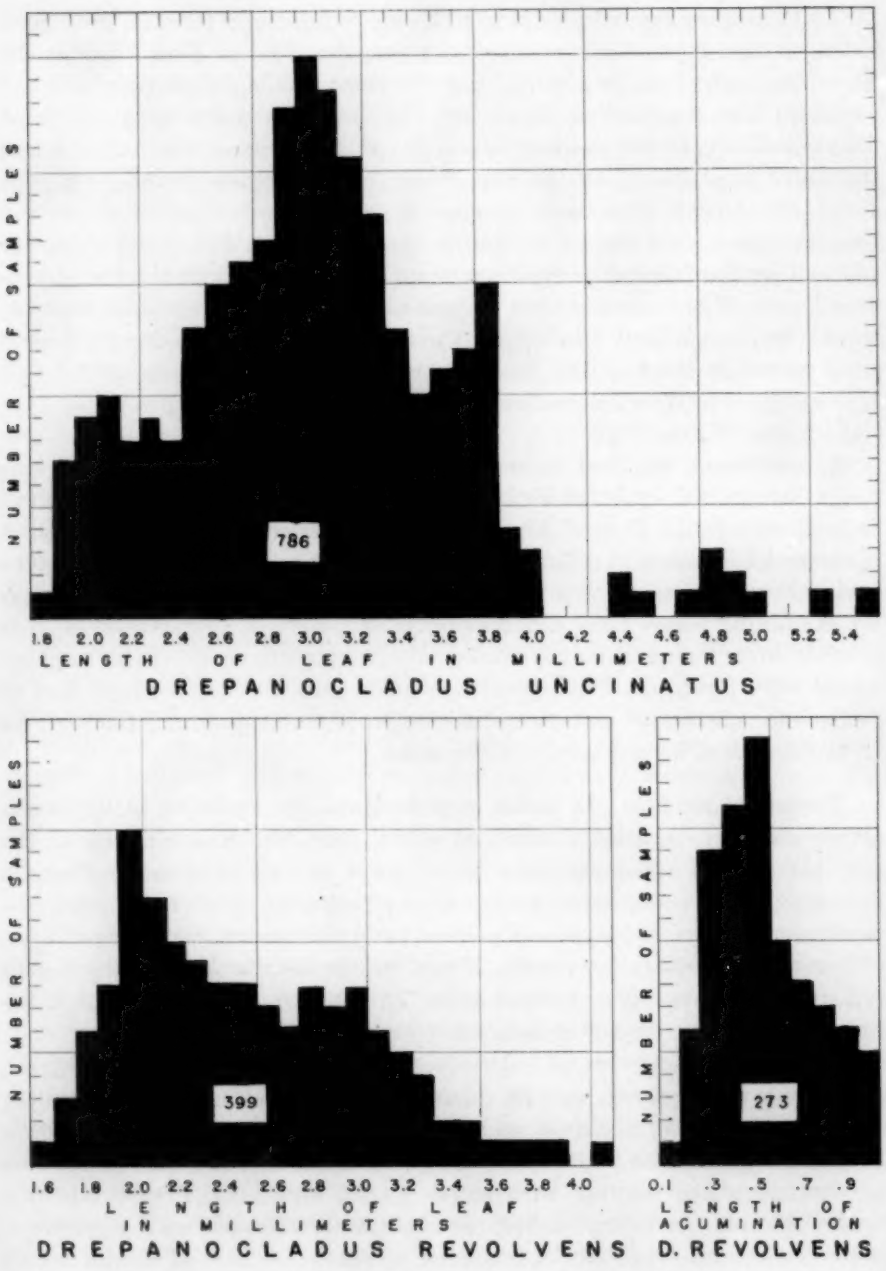
NUMBER OF SAMPLES
786
1.8 2.0 2.2 2.4 2.6 2.8 3.0 3.2 3.4 3.6 3.8 4.0 4.2 4.4 4.6 4.8 5.0 5.2 5.4
LENGTH OF LEAF IN MILLIMETERS
DREPANOCLADUS UNCINATUS
NUMBER OF SAMPLES
399
1.6 1.8 2.0 2.2 2.4 2.6 2.8 3.0 3.2 3.4 3.6 3.8 4.0
LENGTH OF LEAF IN MILLIMETERS
DREPANOCLADUS REVOLVENS
NUMBER OF SAMPLES
273
0.1 .3 .5 .7 .9
LENGTH OF ACUMINATION
D. REVOLVENS

FIG. 2. Statistical data on *Drepanocladus uncinatus* and *D. revolvens*.

collections so named was made. In all these collections leaves of various lengths (2.2, 2.4, 2.5, 3.0, 3.2 mm.) were found in the same clone. The author believes, therefore, that small leaves are minor habitat variations of a large variable population, *D. uncinatus* var. *typicus*. The small group of plants with leaves 4.4–5.5 mm. long belong to *D. uncinatus* var. *subjulaceus*. The large size of the leaves on these plants is constant and correlated with a robust habit, a golden yellow color, and a distinct geographical range (western North America and Quebec and Newfoundland).

Length of leaf and length of acumination of plants known as *D. revolvens* and *D. intermedius* were measured and plotted on the same histogram. This indicated that *D. intermedius,* which had been separated from *D. revolvens* on the basis of its smaller leaves and shorter acumination, was not a natural population. Furthermore, examinations of many leaves from the same plant revealed acuminations varying in length from 0.1 to 0.8 mm. Therefore, on the basis of these observations, the name *D. intermedius* (Lindb.) Warnst. has been excluded and plants previously called *D. intermedius* placed in *D. revolvens*.

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STUDIES IN THE SIMAROUBACEAE—II. THE GENUS SIMAROUBA*

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The genus *Simarouba* was founded in 1775 by Aublet, with *S. amara* Aubl. as the type species. Although it is frequently spelled *Simaruba,* the original spelling, *Simarouba,* must stand. *Simarouba* differs from the related *Quassia* L. and *Simaba* Aubl. in its unisexual flowers and long divergent stigmas, *Simaba* and *Quassia* having the flowers perfect and the single

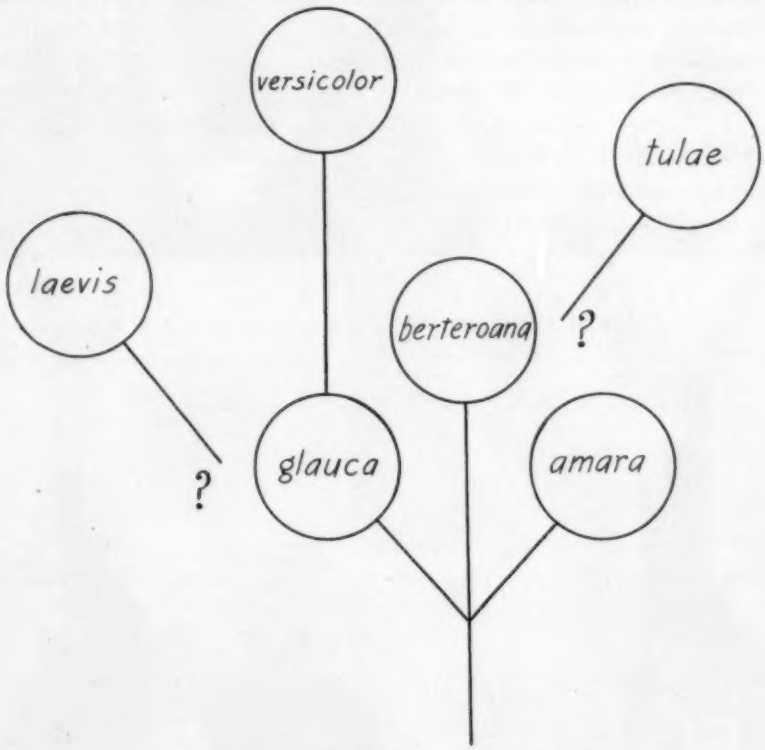

FIG. 1. Supposed phylogeny of *Simarouba.*

stigma capitate or slightly lobed. The gynophore in *Simaba* is usually larger and more conspicuous than in *Simarouba,* and the appendages of the filaments may be much longer, but these characters are not entirely dependable.

Although *Simarouba, Simaba, Quassia,* and the African *Odyendea* form

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an obvious and closely knit group, the origin of the group and the immediate derivation of the genus *Simarouba* are not clear. Within the genus, *S. amara*, *S. glauca*, and *S. Berteroana* are closely related and probably represent divergent end-lines of a common stock. *S. versicolor* is probably derived from *S. glauca*, or at least these two have a common ancestor more recent than the common ancestor of *S. glauca* and *S. amara*. *S. laevis* and *S. Tulae*, although clearly belonging to the genus, are each somewhat isolated, with obscure affinities. *S. Tulae* may be most closely related to *S. Berteroana*, while it might be hazarded that *S. laevis* is derived from *S. glauca*. These relationships are shown diagrammatically in figure 1.

Two sections have been proposed, *Porphyrosimarouba* for *S. Tulae*, and *Eusimarouba* for the rest of the species. If these are to be maintained, a third section should be set up for *S. laevis*, but the genus is so small that division into sections is of doubtful value, and I decline to establish any additional ones.

Nearly 500 herbarium sheets have been available for this study. I wish to thank Dr. H. A. Gleason and Mr. B. A. Krukoff, of the New York Botanical Garden, who have given continued advice and assistance, and Dr. R. T. Major, of Merck Research Laboratory, who has made this study possible. Also I wish to thank the curators of the several herbaria (hereinafter designated by the letters at the left), who have kindly loaned specimens:

A—Arnold Aboretum, Harvard University, Jamaica Plain, Mass.,
F—Field Museum, Chicago, Ill.,
Mich—University of Michigan, Ann Arbor,
MO—Missouri Botanical Garden, St. Louis,
NY—New York Botanical Garden,
US—United States National Herbarium, Washington, D. C.,
Y—Yale University School of Forestry, New Haven, Conn.

Specimens cited as Kr. Herb. are mostly vouchers received by Mr. Krukoff in connection with samples for chemical study.

All measurements of flower parts are taken from specimens restored to normal size by boiling.

SIMAROUBA AUBL.

Trees or shrubs; leaves alternate, pinnately compound; leaflets 3–21, firm, offset or rarely some of them opposite; dioecious; inflorescence a complex mixed panicle, the staminate larger and with more numerous flowers than the pistillate; sepals 5, occasionally 4 or 6, united at the base; petals 5, occasionally 4 or 6, distinct; stamens appendaged at the base, 10, occasionally 8 or 12, in the pistillate flowers much reduced or absent; carpels 5, occasionally 4 or 6, borne on a short broad gynophore or disk, weakly united, with a short common style and divergent stigmas; the staminate flowers with the gynophore present but the carpels absent; ovules 1 in each carpel; fruit of several distinct drupes.

KEY TO SPECIES AND VARIETIES

1. Petals 9–11 mm. long; appendages of the filaments glabrous; leaflets elliptical, broadest near the middle; plant of Puerto Rico.....6. *S. Tulae*.

1. Petals 3.5–7 mm. long; appendages of the filaments with at least a few hairs at the tip, often densely hairy; leaflets either oblong, with parallel sides, or somewhat obovate and broadest above the middle, except sometimes in *S. Berteroana;* plants of South and Central America, Florida (U. S. A.), and the West Indies, but not of Puerto Rico.

2. Leaflets mostly 3–5, sometimes 7, not at all veiny beneath; gynophore of the staminate flowers very short, the filaments inserted essentially at the edge of its top, distinctly not inferior to it; petals about 4.5–5.5 mm. long; anthers about 1.2–1.4 mm. long; plant of Cuba. ..... 5. *S. laevis.*

2. Leaflets mostly 9 or more, sometimes only 7, in *S. Berteroana,* with evident veins beneath except in forms of *S. amara;* gynophore of the staminate flowers relatively well developed, the filaments inserted distinctly below it; plants of general distribution, including Cuba.

3. Appendages of the filaments densely hairy, relatively short and broad, the attached portion no longer than the free portion; free portion of the appendages bent over and closely investing the gynophore, in the staminate flowers; leaflets from minutely rugulose and dull to papillate and glaucous beneath.

4. Petals 4.5–7 mm. long; anthers 1.2–2.0 mm. long; venation various; plants of Haiti, the Dominican Republic, Jamaica, Cuba, the Bahamas, Florida (U. S. A.), southern Mexico, and Central America.

5. Leaflets glaucous beneath, the surface closely papillate; main veins evident as distinct dark lines on the lower surface; leaflets tending to be obtuse or rounded at the apex; anthers 1.5–2.0 mm. long, or sometimes only 1.3 mm. in var. *typica;* plant of Cuba, Jamaica, the Bahamas, southern Florida, southern Mexico, and Central America, as well as occasionally Haiti and the Dominican Republic. ..... 3. *S. glauca.*

6. Leaflets relatively narrow, mostly more than 3 times as long as wide, except for some of the basal ones; plant of Cuba and occasionally Jamaica. ..... 3A. *S. glauca* var. *typica.*

6. Leaflets relatively broad, mostly at least ⅓ as wide as long; range of the species, but uncommon in Cuba. 3B. *S. glauca* var. *latifolia.*

5. Leaflets not glaucous beneath, the lower surface minutely rugulose and punctate, or very minutely papillate; leaflets tending to be abruptly acute at the tip; main veins discernible as faint furrows or as light lines on the lower surface; anthers mostly 1.2–1.4 mm. long; plant of Haiti and the Dominican Republic. ..... 2. *S. Berteroana.*

4. Petals 3.5–4.5 mm. long; anthers 0.7–1.0 mm. long; veins on the lower surface of the leaflets obscure or visible as furrows; plant of South and Central America, and the West Indies as far north as Antigua. ..... 1. *S. amara.*

5. Leaflets glaucous beneath, the surface papillate. 1B. *S. amara* var. *opaca.*

5. Leaflets not glaucous beneath, the surface minutely rugulose and punctate, or very minutely papillate. ..... 1A. *S. amara* var. *typica.*

3. Appendages of the filaments sparsely to sometimes rather densely hairy, relatively long and narrow, the attached portion longer than the short free portion; free portion of the appendages somewhat raised above the gynophore, not closely investing it, in the staminate flowers; petals about 4.5–5.5 mm. long; anthers 1.0–1.4 mm. long; lower surface of the leaflets glaucous, bearing a minute close reticulum of waxy material, the occasional larger than the average

areolae giving a somewhat punctulate appearance under low magnification (often densely hairy, and the reticulum thus obscure).
4. *S. versicolor.*

4. Leaflets conspicuously hairy beneath. .....4A. *S. versicolor* var. *typica.*
4. Leaflets glabrous or nearly so beneath. .....4B. *S. versicolor* var. *pallida.*

SYSTEMATIC TREATMENT OF THE SPECIES

1. SIMAROUBA AMARA Aubl. Pl. Gui. **2**: 860. *pl. 331,332.* 1775.

Tree 7–35 meters high; leaflets mostly 9–21, elliptic-oblong, usually broadly so, with nearly parallel sides, cuneate at the base, rounded to sometimes abruptly short-acuminate at the apex, mostly 6–15 cm. long, 2–6 cm. wide, the lowermost ones sometimes smaller, glabrous, the lower surface dull and rugulose to papillate-glaucous, the veins obscure or showing as furrows; calyx about 1 mm. long or a little more, glabrous or finely puberulent, the broad teeth equaling or shorter than the tube, petals 3.5–4.5 mm. long, green, yellow-green, or sometimes white, appendages of the filaments densely hairy, relatively short and broad, the attached portion no longer than the free portion, which bends over and closely invests the gynophore, in the staminate flowers; anthers 0.7–1.0 mm. long; fruit about 1–1.5 cm. long, ellipsoid, 2-ridged.

1A. SIMAROUBA AMARA Aubl. var. **typica** Cronquist, var. nov.

S. amara Aubl. Pl. Gui. **2**: 860. *Pl. 331, 332.* 1775.
Quassia Simarouba L.f. Suppl. 234. 1781.
Zwingera amara Willd. Sp. Pl. **2**: 569. 1799.

Lower surface of the leaflets minutely rugulose and punctate, or very minutely papillate, dull.

Type: Aublet s. n., French Guiana.

Distribution: Brazil, Bolivia, and Peru, north to Costa Rica, in Central America, and Antigua, in the West Indies.

ANTIGUA[1]: *Box 1415* (US). MONTSERRAT: *Shafer 365* (=*565*), (NY). GUADELOUPE: *Duss 2973* (MO), *3427* (F, NY, US); *Stehle 2587* (US). MARTINIQUE: *Duss 1198* (NY); *Hahn 145* (US). DOMINICA: *Cooper 161* (Mich, US); *Fishlock 38* (MO, NY, US). BARBADOS: *Eggers 7150* (A, US); *Stehle 2982* (NY). GRENADA: *Broadway s. n.*, May 1, 1906 (F, MO, NY). TRINIDAD: *Brooks s. n.* (Kr. Herb. # 16137). BRITISH GUIANA: *Wood s. n.* (Kr. Herb. # 16167). Essequibo: *Smith 2857* (A, MO, NY, US). DUTCH GUIANA: *Stahel s. n.* (Kr. Herb. # 16245). FRENCH GUIANA: *Melinon s. n.* (year 1863) (A). BRAZIL: *Glaziou 17234* (NY). Amazonas: *Ducke 374* (Kr. Herb., Y). Basin of Rio Madeira: *Krukoff 6314* (A, NY, US), *7198* (A, MO, NY, US). Basin of Rio Negro: *Ducke 60* (A, F, MO, NY, US). Basin of Rio Purus: *Krukoff 5240* (A, MO, NY, US). Basin of Rio Solimoes: *Krukoff 8176* (A, MO, NY). Para: *Capucho 470* (F); *Carr 326* (F); *Moss 56* (US). Maranhao: *Froes 32* (US), *1966* (A, MO, NY, US), *11910* (A, NY). Ceara: *Luetzelburg 26343* (F). Bahia: *Curran 11* (US, Y), 21 (Y); *Froes 69* (Kr. Herb.), *97* (Kr. Herb.); *Froes s. n.* (Kr. Herb. # 16715). Matto Grosso: *Krukoff 1462* (A, NY). Minas Geraes: *Barreto 1258* (F). BOLIVIA: La Paz: *Krukoff 10324* (A, MO, NY), *11019* (A, MO, NY). PERU: *Tessman 5431*

[1] In view of the potential economic importance of *Simarouba amara* and *S. glauca*, it has been thought desirable to cite all specimens examined. This has been done at the expense of the Research Department of Merck & Co., Inc.

(NY). San Martin: *Klug 3741* (A, MO, NY, US). Loreto: *Klug 323* (F, NY, US), *639* (F, NY, US), *3207* (A, F, MO, NY, US). CANAL ZONE: *Carpenter 42* (F); *Starry 144* (F). COSTA RICA: San Jose: *Skutch 2510* (A, Mich, MO, NY, US), *4032* (A, MO, NY). Limon: *Standley & Valerio 48428* (US).

1B. SIMAROUBA AMARA Aubl. var. OPACA Engl. Nat. Pfl. **3**(4): 213. 1896.

S. opaca Radkl. ex Engl. Nat. Pfl. ed. 2 **19a**: 374. 1931.

Lower surface of the leaflets papillate, glaucous.

Type: "*in Nordbrasilien* (*Para, Alto Amazonas*) *und Bahia, auch cultiviert bei Rio de Janeiro.*"

Distribution: Brazil to British Honduras; apparently absent from the West Indies.

GUATEMALA: El Peten: *Cook & Martin 75* (US). Jutiapa: *Standley 75955* (F). BRITISH HONDURAS: *Hope 1* (F, Y); *Gentle 1870* (A, F, Mich, NY), *2751* (A, Mich, NY), *3280* (A, Mich, MO, NY); *Schipp 123* (F, MO, NY, US); *Stevenson s. n.* (Kr. Herb. # 16180). HONDURAS: Atlantida: *Standley 52807* (A, US), *55546* (A, US). EL SALVADOR: La Union: *Beetle 26257* (A, MO). VENEZUELA: *Tate 1152* (NY). Bolivar: *L. Williams 11774* (F, Kr. Herb., US). BRITISH GUIANA: Mount Roraima: *Tate 241* (NY). BRAZIL: Amazonas: Basin of Rio Branco: *Kuhlmann 3038* (US). Basin of Rio Negro: *Krukoff 7932* (A, MO, NY). Para: *Spruce 442* (NY). Bahia: *Blanchet 2727* (MO, NY); *Curran 98* (US); *da Cunha s. n.* (Kr. Herb. # 16483).

Simarouba amara has long been confused with *S. glauca*, but the two are amply distinct. The differences in size of anthers and petals are of critical importance. The petals in *S. amara* are dull yellow-green, or sometimes whitish, while those of *S. glauca* are commonly brighter yellow, not infrequently with a touch of orange or red. *S. amara* is a large tree of the rainforest; *S. glauca* is commonly a large shrub or small tree, often of somewhat drier and more open habitats. The key difference in leaf venation is not entirely constant; individuals having leaves seemingly intermediate between *S. glauca* and *S. amara* var. *opaca* are clearly referable to *S. glauca* on the basis of flower structure.

2. SIMAROUBA BERTEROANA Krug & Urb. Bot. Jahrb. **15**: 306. 1892.

Tree; leaflets mostly 7–9, relatively widely spaced, glabrous, cuneate and usually slightly oblique at the base, usually abruptly short-pointed at the apex, narrowly elliptic to broadly elliptic-ovate, about 5–10 cm. long, 1.5–3.5 cm. wide, the lower surface dull and minutely rugulose, very minutely papillate, the veins showing as faint furrows or sometimes more evident lines; calyx a little over 1 mm. long, sometimes pruinose-glaucous, the broad rounded lobes equaling or exceeding the tube and sometimes finely ciliolate on the margins; petals yellow-green, about 4.5–6 mm. long; appendages of the filaments like those of *S. amara* and *S. glauca;* anthers about 1.2–1.4 mm. long; fruit about 1.5–2 cm. long, 2-ridged.

Type: Bertero 64, Dominican Republic (NY—fragment and photo).

Distribution: Haiti and the Dominican Republic.

HAITI: *Desert s. n.* (Y); *Ekman H3036* (US); *Leonard 4265* (NY, US). DOMINICAN REPUBLIC: *Fuertes 47* (F, MO, NY, US); *Jimenez s. n.* (Kr. Herb. # 16334); *Schiffino 92* (US, Y).

This species combines the characters of *S. amara* and *S. glauca*, but seems genetically stable. In leaf texture and venation it resembles *S. amara;* in petal size it simulates *S. glauca*. The anthers are larger than in *S. amara*, and about at the lower size limit for *S. glauca*. The pronounced tendency toward abruptly acute leaflets, a feature found only occasionally in *S. amara*, and scarcely at all in *S. glauca*, suggests that it is a residual stock rather than a stabilized hybrid.

3. SIMAROUBA GLAUCA DC. Ann. Mus. Paris **17**: 424. 1811.

Large shrub, or small tree, rarely larger and as much as 18 meters high; leaflets mostly 8–16, cuneate at the base, rounded to occasionally acutish at the apex, narrowly obovate to broadly elliptic-oblong, mostly 4–10 cm. long, 12–50 mm. wide, the lowermost ones sometimes smaller; lower surfaces of the leaflets glabrous to sometimes moderately appressed-hairy, conspicuously papillate-glaucous and evidently reticulate-veiny, the veins appearing dark in herbarium specimens; calyx a little over 1 mm. long, glabrous, often also somewhat pruinose-glaucous, the broad rounded lobes equaling or exceeding the tube, sometimes finely ciliolate on the margins; petals 4.5–7 mm. long, mostly yellow-green, sometimes brighter yellow and with an orange-red midstripe; appendages of the filaments much like those of *S. amara;* anthers 1.5–2.0 mm. long, or sometimes only 1.3 mm. long in var. *typica;* fruit about 1.5–2.0 cm. long, ellipsoid, 2-ridged.

3A. SIMAROUBA GLAUCA DC. var. **typica** Cronquist, var. nov.

S. glauca DC. Ann. Mus. Paris **17**:424. 1811.
Quassia glauca Spreng. Syst. 2:319. 1825.

Leaflets narrower in shape and averaging smaller than those of var. *latifolia*, mostly more than three times as long as wide, except sometimes some of the basal ones; anthers sometimes a little smaller than in var. *latifolia*.

Type: Humboldt & Bonpland s. n., near Havana, Cuba.
Distribution: Cuba, and apparently occasionally in Jamaica.

CUBA: *Gill & Whitford s. n.* (year 1925) (Y); *Leon 2597* (NY); *Rugel 209* (NY). Pinar del Rio: *Britton & Cowell 9915* (NY). Isla de Pinos: *Britton, Wilson & Leon 15271* (NY). Matanzas: *Britton & Wilson 14048* (NY, US). Santa Clara: *Acuna s. n.* (Kr. Herb. # 16053); *Britton, Britton, & Wilson 5570* (NY, US); *Britton, Cowell, & Earle 10304* (NY); *Britton, Earle, & Wilson 4624* (NY, US); *Britton & Wilson 5534* (NY, US), *5658* (NY); *Jack 4194* (A, NY), *4511* (A), *4834* (A, NY); *Rehder 1112* (A), *1213* (A); *Shafer 12312* (NY, US). Camaguey: *Shafer 318* (NY, US), *1086* (NY, US). JAMAICA: *Harris 9551* (NY).

3B. SIMAROUBA GLAUCA DC. var. **latifolia** Cronquist, var. nov.

S. officinalis DC. Ann. Mus. Paris **17**:423. 1811, in part.
S. medicinalis Endl. Med.–Pfl. Osterreich. 528. 1842.
S. officinalis DC. forma *glabra* Krug & Urb. Bot. Jahrb. **15**:305. 1892.

Leaflets broader and averaging larger than those of var. *typica*, mostly at least 1/3 as wide as long.

A var. typico differt foliolis latioribus, latitudine saltem tertiam partem longitudinis aequanti.

Type: Curtiss 5625, Key West, Florida, April 18, 1896 (NY); isotypes at MO, US.

Distribution: Central America (Costa Rica) to Mexico (Oaxaca); southern Florida (U.S.A.); Bahama Islands; Jamaica; occasional in Cuba, Haiti, and the Dominican Republic.

MEXICO: *Rovirosa 730* (US). Oaxaca: *L. Williams 9375* (F). Tabasco: *Matuda 3116* (A, F, Mich, NY). Yucatan: *Gaumer 439* (A, F, MO, NY, US), *23252* (A, MO, NY, US), *23583* (F, MO, US), *24111* (F, MO, US). BRITISH HONDURAS: *Brown 33* (F, Y); *Carnegie Institute & U. of Michigan 3rd Biological Exp. 4350* (F, Mich); *Gentle 381* (F, Mich, US), *417* (A, F, Mich, MO, US), *1200* (A, Mich, MO, NY, US); *Heyder 8* (US, Y); *Lundell 4350* (F); *Turner s. n.* (Kr. Herb. # 16301). GUATEMALA: *Deam 195* (A, Mich); *Friedrichsthal 923* (F); *Record & Kuylen G128* (US, Y). El Peten: *Bartlett 12662* (A, Mich, NY, US); *Lundell 2185* (A, F, Mich, US) *2234* (A, F, Mich, US); *Mercedes 363* (Mich). Baja Verapaz: *Cook & Doyle 92* (US); *Kellerman 6634* (F). Izabal: *Kellerman 4512* (F, US); *Steyermark 38125* (F). El Progresso: *Popenoe 982* (US). Zacapa: *Standley 72030* (F); *Steyermark 29303* (F). Jalapa: *Kellerman 7004* (F), *7896* (F, NY). Amatitlan: *Morales 738* (US). Jutiapa: *Standley 60550* (F). HONDURAS: Camayagua: *Edwards 91* (A, F), *373* (A, F, US), *571* (A, F, US). Yoro: *Standley 55047* (A, US). EL SALVADOR: *Villacorta 8136* (US). La Libertad: *Standley 23222* (US). San Salvador: *Calderon 257* (NY, US); *Renson 233* (NY, US). San Vincente: *Standley 21232* (US). La Union: *Standley 20692* (NY, US). NICARAGUA: Leon: *Baker 2266* (A, MO, NY, US). Managua: *Chavez 173* (US); *Garnier 3009* (A). Masaya: *Maxon 7674* (US). COSTA RICA: Puntarenas: *Quiros-Calvo 798* (F). UNITED STATES: Florida: *Bessey 20* (A); *Blodgett s. n.* (NY); *Curtiss 439* (Mich, MO, NY, US), *5625* (MO, NY, US), *s. n.* (March, 1882) (A); *Duckett 218* (A, NY, US); *Farnum s. n.* (February, 1930) (Mich, MO, US); *Fennell 329* (A, NY), *Garber s. n.* (year 1877) (MO, US); *J. A. Harris C21345* (US); *A. H. Howell 875* (US); *MacDonald 34* (Y); *Moldenke 823* (MO, NY, US), *3669* (NY); *Mosier 379* (US); *O'Neill 7585* (A, NY, US), *s. n.* (August 21, 1929) (MO, US); *Pollard, Collins, & Morris 187* (NY, US); *Rehder 713* (A); *Rugel 107* (MO, US), *108* (NY, US); *Safford & Mosier 89* (US), *90* (US); *Sargent s. n.* (April 6, 1886) (A), (April 13, 1886) (A), (April 20, 1886) (A); *Simpson 346* (US), *564* (NY), *564a* (US); *Small 7451* (NY, US), *8766* (NY), *8842* (NY); *Small, Mosier, & Small 6428* (NY); *Small & Nash 16* (NY); *Small & Small 4712* (MO, NY). BAHAMA ISLANDS: *Brace 1648* (NY), *3913* (NY), *6795* (NY); *Britton & Millspaugh 2649* (NY); *Small & Carter 8725* (NY, US). CUBA: *Oriente: Britton & Cowell 12533* (NY, US). Santa Clara: *Jack 4565* (cultivated) (A, US), *5103* (cultivated) (A, US). DOMINICAN REPUBLIC: *Valeur 845* (MO, NY); *Wright, Parry, & Brummel 174* (F, US). HAITI: *Cook 12* (US). JAMAICA: *R. C. Alexander s. n.* (year 1850) (MO, NY); *Britton 3767* (NY); *Harris 5931* (NY), *8664* (NY, US), *9358* (A, NY); *Hart 1053* (F, US), *s. n.* (US).

Some of the Central American plants (exemplified by *Edwards 571,* Camaygua, Honduras) have conspicuously longer (up to 7 mm.) and more brightly colored petals than usual, and the Edwards plant is reported to be a tree 60 feet high; without additional material it is difficult to say whether these represent a true variety or merely an unusual form.

S. officinalis DC. was based on at least two elements; most of the specimens cited would seem to belong to a slightly pubescent phase of *S. glauca* var. *latifolia,* but the extensive synonymy given all refers to *S. amara.*

4. SIMAROUBA VERSICOLOR A. St. Hil. Pl. Us. Bras. *pl. 5.* 1824.

Small tree mostly 4–5 meters high; leaflets mostly 9–16, narrowly obovate to broadly oblong or elliptic-oblong, cuneate at the base, rounded to acutish at the tip, mostly 4–10 cm. long and 1.5–3.5 cm. wide, the lowermost ones sometimes smaller, the lower surface provided with a minute close waxy reticulum that is ordinarily readily visible under a magnification of 25 diameters (unless obscured by pubescence), the occasional larger than average areolae often giving a minutely punctulate appearance under low magnification, the surface varying from otherwise glabrous to densely spreading-hairy; calyx about 1 mm. long or a little more, glabrous or sparsely hirtellous, the broad rounded lobes about as long as the tube, often ciliolate on the margins; petals about 4.0–5.5 mm. long; appendages of the filaments sparsely to sometimes rather densely hairy, relatively long and narrow, the attached portion longer than the short free portion, which is raised somewhat above the gynophore, in the staminate flowers, instead of closely investing it; anthers about 1.0–1.4 mm. long; fruit about 2–2.5 cm. long, ellipsoid or ovoid, 2-ridged.

4A. SIMAROUBA VERSICOLOR A. St. Hil. var. **typica** Cronquist, var. nov.

S. versicolor A. St. Hil. Pl. Us. Bras. *pl. 5.* 1824.
S. versicolor A. St. Hil. var. *angustifolia* Engl. in Mart. Fl. Bras. **12**(2): 226. 1874.

Lower surface of the leaflets more or less densely spreading-hairy.

Type: "*Dans les paturages de la province de Minas Geraes, voisins du Rio-de-S.-Francisco,*" Brazil.

Distribution: Semi-open places; eastern Brazil, from Maranhao to Minas Geraes, thence westward to Bolivia.

BRAZIL: *Herb. Drake s. n.* (F); *Glaziou s. n.* (A). Ceara: *Gardner 1513* (NY, US); *Luetzelburg 25828* (F). Bahia: *Blanchet 3142* (NY); *Luetzelburg 1456* (NY). Maranhao: *Snethelage 723* (US). Matto Grosso: *Malme 1537* (US); *Martius Herb. 572* (MO, NY). Rio de Janeiro: *Glaziou 10463* (US). BOLIVIA: *Kuntze s. n.* (July, 1892) (NY).

4B. SIMAROUBA VERSICOLOR A. St. Hil. var. PALLIDA Engl. in Mart. Fl. Bras. **12**(2): 226. 1874.

Lower surface of the leaflets glabrous.

Type: "*In prov. Goyaz inter arbuscula tortuosa pr. Paracaitu, et in Chapado de S. Marcos prov. Minas Geraes,*" Brazil.

Distribution: Semi-open places; eastern Brazil, from Ceara and Piauhy to Minas Geraes, thence westward to Bolivia.

BRAZIL: *Pohl 935* (F) Ceara: *Ule 9044* (US). Piauhy: *Dahlgren 981* (F). BOLIVIA: El Beni: *Rusby 1361* (NY), *1714* (NY, US). Santa Cruz: *Steinbach 6410* (F), *7210* (F, MO, NY), *7269* (F, MO, NY).

The peculiar waxy reticulum on the lower surface of the leaflets is quite enough to identify either variety of this species, even in the absence of flowers. From the available specimens it would seem that var. *typica* is more common in Brazil, while var. *pallida* is more common in Bolivia. No specimens have been found to connect definitely the Brazilian with the Bolivian range, but such a connection doubtless exists.

5. SIMAROUBA LAEVIS Griseb. Cat. Pl. Cub. 49. 1866.

Shrub or small tree, mostly 2–6 meters high; leaflets mostly 3–5, sometimes 7, glabrous, obovate or elliptic, cuneate at the base, rounded at the summit, 3–7 cm. long, 1.5–3 cm. wide, the lower surface dull, minutely rugulose and punctulate, not at all veiny, or very obscurely so; calyx about 1.5 mm. long or a little more, glabrous except sometimes for some ciliae on the margins of the broad rounded lobes, which slightly exceed the tube; petals about 4.5–5.5 mm. long, reported to be white; filaments inserted essentially at the edge of the top of the very short gynophore, in the staminate flowers; appendages thick, firm, erect, the free portion longer than the short attached portion; anthers about 1.2–1.4 mm. long; fruit about 1.5–2 cm. long, ellipsoid, 2-ridged.

Type: Wright 2187, eastern Cuba (MO, NY, fragments).
Distribution: Cuba.

CUBA: *Britton, Britton, & Shafer 703* (NY). Pinar del Rio: *Leon & Roig 13542* (NY). Habana: *Leon 2931* (NY), *5204* (NY); *Leon & Cesaere 8938* (NY). Matanzas: *Britton, Britton, & Wilson 14068* (NY, US). Santa Clara: *Britton, Britton, & Wilson 6204* (NY); *Britton & Cowell 10194* (NY), 13282 (NY); *Jack 5417* (A). Oriente: *Wright 1159* (NY).

6. SIMAROUBA TULAE Urb. Jahrb. Bot. Gart. Berlin **14**: 245. 1886.

Shrub or tree, mostly 2–8 meters high; leaflets mostly 5–10, offset or sometimes some of them opposite, glabrous, cuneate at the base, abruptly acuminate at the apex, elliptic, broadest about the middle, 5–11 cm. long, 1.5–5 cm. wide, dull, very minutely papillate, and often somewhat brownish, on the lower surfaces; inflorescence relatively broad and short; calyx about 1.5 mm. long or more, glabrous, the broad obtuse or rounded lobes equaling or exceeding the tube, petals about 9–11 mm. long, red; appendages of the filaments relatively long and slender, glabrous, the attached portion longer than the short free portion; anthers about 1.5 mm. long, or a little more; fruit strongly flattened, broadly and asymmetrically obovate, 2–3.5 cm. long, red.

Type: Wydler 418, prope Maricao, Puerto Rico.
Distribution: Puerto Rico.

PUERTO RICO: *Britton & Cowell 4221* (NY, US): *Britton, Cowell, & Brown 4452* (MO, NY, US); *Britton & Marble 679* (NY, US); *Britton, Stevens, & Hess 2463* (NY, US); *Eggers 1284* (US); *Gregory 54* (NY); *Hess 1461* (NY), *2208* (NY); *Hioram s. n.* (July, 1931) (NY); *Holdridge 224* (NY); *McClelland 9134* (NY); *Sargent 605* (US); *Sintensis 277* (US), *297* (US), *1329* (US), *2550* (US), *4392* (US), *4683* (F, MO, NY, US).

EXCLUDED SPECIES

Simarouba excelsa DC. Ann. Mus. Par. **17**: 424. 1811. = *Picrasma excelsa* (Sw.) Planch.
Simarouba monophylla Oliver Ic. Pl. *pl.* 1387. 1882. = *Simaba* sp.
Simarouba obovata (Spruce ex Engl.) Engl. Nat. Pfl. **3**(4): 212. 1896. = *Simaba obovata* Spruce ex Engl.

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SOME STATISTICS OF ACHRAS ZAPOTA LEAVES, BRITISH HONDURAS[1]

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PURPOSE OF THE STUDY

The taxonomic status of the *Achras* complex in Central America is still in need of further investigation. Of this complex *Achras zapota* is the most commonly recognized species.[2] This tree is the source of the chicle of commerce, which is used as a base for chewing gum and is derived from the coagulation of the latex of the bark. The gathering of the latex by professional chicleros is an industry of considerable local importance. *Achras zapota* also produces the fruit known as sapodilla, found in local markets in many parts of the tropics. The wood of *Achras* is generally recognized as being durable, and it is claimed that certain beams in Mayan ruins, probably 1000 to 1500 years old, are still sound. Furthermore, *Achras* is a forest tree of considerable importance in the local vegetation, both because of its numbers and its size. For these reasons, the recognition of species, strains and types is a matter of practical and academic significance.

Both the existing literature on the *Achras* complex and treatments of the genus in regional manuals and local native opinion emphasize the importance of leaf shape in the segregation of taxonomic entities. Furthermore, differences in normal leaves of the sapodilla are such that their taxonomic significance deserves further investigation. The purpose of this paper is to present certain statistics on normal leaf variation in a population of *Achras zapota*, as an impartial contribution to our knowledge of that segregate. Such statistics may serve as a base for evaluation of botanical collections made elsewhere. Data on floral variation and evaluation of floral variation are not here considered.

[1] Contribution No. 1 from the Chicle Development Company Experiment Station. Professor C. C. Carpenter, Syracuse University, has reviewed the use of statistical methods in this study. Comments on the manuscript have been received from Professors R. R. Hirt, J. L. Lowe, H. F. A. Meier, and H. K. Phinney, N. Y. State College of Forestry, and from Professor Stanley A. Cain, University of Tennessee.

[2] Gilly (Trop. Woods **73**: 1–22. 1943), has shown that the name *Achras zapota* is untenable, and has proposed *Manilkara zapotilla* (Jacq.) Gilly to replace it. He has split *Achras zapota* into ten species, primarily on the basis of floral characters, of which species nine are new. Because the present author is not yet in the position to recognize these additional species, because Gilly himself writes that his "paper must be regarded as only a preliminary step toward the solution of the Sapodilla-Nispero complex," and because the old name is firmly entrenched in the practical literature, he is retaining the established binomial pending further investigations.

An additional purpose of this study is to test for significant leaf differences between the so-called "color varieties" of *Achras zapota*. These color varieties, the *blanco* (white), the *colorado* (red), and the *morado* (blue) are generally distinguished without hesitation by native chicleros. The distinctions, however, are obscure and inconstant to botanists. Nevertheless it seems to be a scientific practice to place faith in a tropical native's ability to separate species, a situation sometimes carried to such extremes as would not be accepted in north temperate regions. The very seriousness with which the situation is being accepted for *Achras* makes a report of this kind desirable.

On the basis of the literature and the author's studies in the Yucatan peninsula, it would appear that identification of a color variety represents a chiclero's *opinion* on the latex yield of the tree *if* it were to be tapped. Since commercial tapping is unsupervised, there is no check on a chiclero's determination, although past studies by the Chicle Development Company indicate that his opinion is not to be taken seriously. The basis of recognition of the varieties is variously reported in the literature, and differs according to region and the individual chiclero. Leaf features are mentioned repeatedly, as well as external bark, color of internal bark, site, form of tree, number of previous tappings, and type of fruit. The author has found different chicleros to give different determinations for the same tree, and has found a chiclero to change his determination on closer inspection of a tree. A test machete cut, permitting flow of latex, convinces the chiclero, but not the botanist, as to whether it is a low-yielding red, a high-yielding white, or a very high-yielding blue.

The chicle industry has long recognized that trees differ extremely in the quantity of latex they will yield. It takes no mystic or unusual perspicacity on the part of a field botanist to observe certain correlations between site and morphologic features of the trees. Trees of thin rocky soil and of seasonally parched "akalches" are small, short-boled, open-crowned, limby, exposed to wind, light, and dryness, with deeply fissured bark, and a small amount of latex-yielding inner bark. Trees of deep soil are large, long-boled, close-crowned, in a dense moist shady forest, with shallowly fissured bark, and a greater amount of inner bark. The xeric form is usually the chiclero's colorado, the hygric form is usually the blanco.

FIELD METHODS

The field investigations were carried out in April, 1942, on the Tower Hill East Estate, a unit of the Honey Camp Experimental Forest of the Chicle Development Company Experiment Station in northern British Honduras. The property belongs to the Chicle Development Company of New York, Central American subsidiary of the Beech-Nut Packing Co. and the American Chicle Co. The Tower Hill East Estate was originally purchased

as a typical example of British Honduras sapodilla forest. For statistical purposes one may consider that any other sample of such forest had an equal chance of serving for this study.

The populations sampled were along two arbitrarily chosen foot trails, one in general upland, the other in akalche. The course of the trails bore no relation to local topography, and it may be considered that all trees in the Estate had equal chances of occurring along them.

Thirty-five permanently located trees were used in this study, chosen for purposes of comparing the color varieties, and with as much adherence to the principles of random sampling as the peculiar conditions permitted. Four assumedly homogeneous populations were considered: Upland White, Upland Red, Upland Blue, and Akalche Red. No white or blue trees were found in akalche. For each population, the first 10 trees occurring on the line of travel were accepted (except that only 5 of the rare blues were found). About 6 trees were passed which were difficult or dangerous to climb because of luxuriant lianas or of decay resulting from severe tappings, both of which characteristics were assumed to have no correlation with possible botanical differences. Recognition of the color varieties was by an unusually competent and intelligent chiclero.

From each of the 35 trees, foliage was obtained from approximately midheight of the crown, cut by a chiclero in the presence of the author. Specified location within the crown may have been unnecessary, since it appeared by observation that there was no apparent difference between the types of foliage growing in different parts. The entire crown of *Achras* is open, limby, usually rising above the surrounding vegetation, and well exposed to light in all its parts.

From 1 to 5 small branches were cut by the chiclero, and from them material for herbarium specimens was taken. It is characteristic of *Achras zapota* that the foliage is grouped at the ends of twigs in spreading rosettes (forming a pattern against the sky that aids in field identification), and 10 such rosettes were chosen at random from each tree. In conformity with the plan of this study for sampling only the normal foliage, certain dwarfed, curled, diseased, or abnormally large rosettes were discarded. Every investigator who has carefully observed the full variation of leaves on any one tree realizes that although close to 100 per cent of the foliage forms an intergrading mass, there are certain extremes—as would be midgets and giants in a human population—which can be eliminated in all except very large sampling techniques, here impractical. These leaf abnormalities appeared consistently in all trees, and did not differentiate the trees. Furthermore, the elimination of this small percentage from the analysis affected only the extreme range, a statistic which has not been considered of botanical importance. As a general observation, it may be said that there was sometimes an

obvious individuality of leaf type on a single tree. Such apparent individuality was not carried over to any second tree or group of trees, and careful observation of the foliage of additional trees made it appear that it was nothing more than one phase of varying conditions. The leaf features for statistical treatment, however, were chosen with this individuality in mind.

Rosettes both with new light green foliage and with old dark green foliage were taken. At this season, the early part of the dry season, fall of old leaves and growth of new leaves had been so rapid that approximately three-quarters of the trees showed only new foliage (the light color of which is another aid in field identification). It was determined by observation of rosettes with leaves of both ages that the new set had already attained their full areal growth, and consequently the classes have not been segregated in this study. The young thin leaves are sometimes larger than the old thick leaves, and it is possible that there is a small seasonal variation, with the larger leaves being formed in the period of most rapid growth.

After being dried as herbarium material, and after the leaves had regained enough moisture from the atmosphere that they were no longer brittle, 2 leaves were selected from each rosette for detailed study. Although there was generally only minor variation in size within a rosette, leaves of medium length were deliberately chosen, in accordance with the plan to characterize variations in normal foliage.

By the application of the methods above described, material was at hand consisting of 700 Items (leaves), representing 35 Samples (trees, each being a numbered botanical collection, now deposited in the herbarium of the New York Botanical Garden), further representing 4 assumed Populations (Upland White, Upland Red, Upland Blue, and Akalche Red), later to be compared as 4 Population-pairs (Upland White–Upland Red, Upland White–Upland Blue, Upland Blue–Upland Red, and Upland Red–Akalche Red).

OBTAINING THE BASIC DATA

All measurements on each Item were made to the nearest millimeter with a celluloid metric scale. Work sheets were prepared and data recorded which led either directly or indirectly to a characterization of the following 6 Features (fig. 1):

1. Blade-length. The full length of the leaf-blade was measured from the point of attachment of the petiole to the leaf-tip. Although the leaf-blade base in *Achras zapota* is generally acute, no difficulty was experienced in determining its terminus. In some leaves, one side extends proximally for a measurable distance more than the other side. In such cases, measurement was begun half-way along the extension. Frequently the midrib of the leaf was slightly curved, so that an exact measurement of its length was difficult. If the curve was definitely at one end or the other, a correction was per-

mitted by placing the metric scale along a hypothetically straightened line; if a slight curve occurred throughout, a correction was estimated.

2. Midlength-width. The width of the blade at a point midway along its length is always obtainable without difficulty, since the margins of the leaf are entire and never sinuate except when diseased.

3. Greatest-width. The greatest-width is described as occurring either at the midlength, or proximally or distally from it. Furthermore, it can occur at one particular point along the length, or it can extend along the leaf for various distances. In *Achras,* when the greatest-width was not at midlength, it was measurable at a point; when the greatest-width was at midlength, it sometimes extended proximally or distally, forming a leaf with partly parallel sides. When such parallel sides were largely distal from the midlength—giving the illusion of its being oblanceolate—the shape is here referred to as abelliptic; when such sides were proximal, the shape is adelliptic.

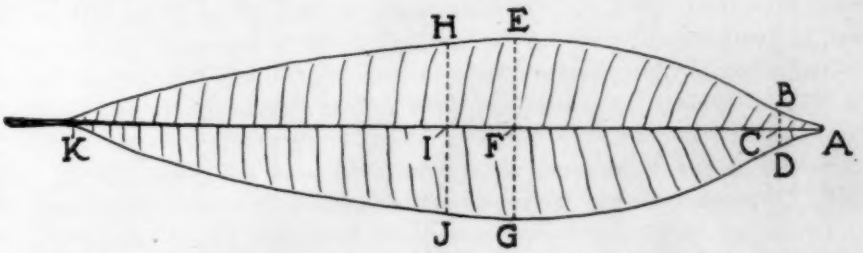

FIG. 1. Diagram of a leaf of *Achras zapota,* showing the 6 Features investigated in this study. Blade-length, AK. Midlength-width, HIJ (I is at midlength). Greatest-width, EG. Degree of lengthwise eccentricity, FI/AK. Degree of breadthwise eccentricity, (EG–HJ)/HJ. Apex-width, BD (AC, 1 cm.). Drawing by L. Partelow, Draftsman, Syracuse, N. Y.

4. The Degree of Lengthwise Eccentricity (DLE). This Feature was developed in order to obtain a serviceable measure of the departure of the greatest-width from the midlength, i.e., the degree to which the greatest-width approached either end of the blade. The distance was measured along the midrib between the midlength and the greatest-width. This figure was converted to a percentage by dividing by the full blade-length.

5. The Degree of Breadthwise Eccentricity (DBE). Comparable to DLE, DBE is designed to express the increase in width of a leaf beyond the width it possesses at midlength. The difference between midlength-width and greatest-width is computed. This figure is divided by the midlength-width in order to give a percentage which can be considered in relation to that midlength. Expressed as a formula,

$$\text{DBE} = \frac{(\text{greatest-width}) - (\text{midlength-width})}{\text{midlength-width}}.$$

6. Apex-width. The type of apex is frequently distinctive of different populations of plants. It is frequently referred to as being rounded, obtuse, acute, acuminate, or attenuate, and emarginate or apiculate. In the populations studied, all leaves were emarginate, although some were conspicuously more so than others. For purposes of quantitative measurement of the nature

TABLE 1. *Leaf-shape types in the 35 samples of Achras zapota.*

Bot. coll. no.	Number of leaves in each leaf-shape type				
	Oblanceolate	Abelliptic	Elliptic	Adelliptic	Lanceolate
42–137	9	3	3	4	1
42–138	11	5	4	0	0
42–139	8	6	5	1	0
42–140	15	1	4	0	0
42–141	15	2	3	0	0
42–142	19	1	0	0	0
42–143	13	3	4	0	0
42–144	6	8	5	1	0
42–145	15	2	3	0	0
42–146	12	7	1	0	0
42–148	16	3	1	0	0
42–149	4	6	10	0	0
42–150	2	3	11	4	0
42–151	8	5	7	0	0
42–152	11	5	4	0	0
42–153	3	8	5	4	0
42–154	11	7	2	0	0
42–155	1	6	11	2	0
42–156	17	2	1	0	0
42–157	8	6	6	0	0
42–158	13	5	2	0	0
42–158A	7	7	5	1	0
42–159	11	4	4	1	0
42–160	6	5	8	1	0
42–161	11	4	5	0	0
42–168	8	4	6	2	0
42–169	7	8	4	1	0
42–170	15	4	1	0	0
42–171	12	6	2	0	0
42–172	16	3	1	0	0
42–173	4	7	7	1	1
42–174	6	8	6	0	0
42–175	15	5	0	0	0
42–176	10	7	3	0	0
42–177	20	0	0	0	0

of the leaf tip, the concept of apex-width was developed, and now defined as the width of the leaf 1 cm. from the tip. This distance is correlated with such qualitative terms as rounded, acute, and attenuate. It is not to be overlooked, however, that it ignores the condition of the sides of the triangle of which the apex-width is the base. Such sides may be straight, concave, or convex, each resulting in a distinctively appearing tip.

THE DATA AND ANALYSES

All calculations in this study were carried out for the author by Hartley K. Phinney, New York State College of Forestry, with the exception that figures for DLE and DBE in table 1, Items 1 through 160, are by Mrs. Dorothy Thomson of Belize, British Honduras.

Characteristics of the Items. According to the methods outlined above, data have been obtained concerning the 6 Features for each of the 700 Items. These were utilized in the computations presented in tables 2–4.

Characteristics of the Samples. Each Sample (tree) contains 20 Items (20 leaves). The leaf-shape types within each Sample are summarized in table 1. Furthermore, for each of the 35 Samples, 3 characteristics have been computed for each of the 6 Features. These are: (1) the *mean* of the measurements; (2) the *range* of the measurements; and (3) the *standard deviation* of the measurements. These statistics are presented in table 2.

Characteristics of the Populations. For each of the 4 Populations, Upland White, Upland Blue, Upland Red, and Akalche Red, 3 characteristics have been computed for each of the 6 Features. These are: (1) the *mean of the sample means;* (2) the observed *range of the sample means;* and (3) the *standard error of the sample means.* These statistics are presented in table 3.

Characteristics of the Population-Pairs. For each of the 4 Population-pairs, 3 characteristics have been computed for each of the 6 Features. These are: (1) the *difference between means of sample means;* (2) the *standard error of the difference between means of sample means;* and (3) the ratio t. These statistics are presented in table 4.

SIGNIFICANCE OF THE VALUES OF t

The 24 values of t computed in the preceding section have been compared to their respective 5 per cent and 1 per cent levels and adjudged "non-significant" or "significant" at each level, according to D. D. Paterson, "Statistical Technique in Agricultural Research," New York, N. Y. Twenty-three of the values were found non-significant; only one was significant, as shown in table 4.

In each instance of non-significance of t, it may also be said that the respective difference between means of the 2 Populations is too small to be considered significant. Further evidence is necessary to determine if the mean actually indicates 2 distinct Populations of the respective Feature. Until that time it may be assumed that the difference is only an incident of sampling from a single normally variable Population.

The single instance of significance of t at the 5 per cent level indicates a significant difference between blade-length means of Upland Red and Upland White Populations. From another point of view, this value of t indicates that the relatively wide difference of means will occur—assuming

TABLE 2. *The characteristics of the 35 samples of Achras zapota.*

Bot. coll. no.	Site	Tree type	Features																	
			Blade-length, cm.			Midlength-width, cm.			Greatest-width, cm.			DLE,[a] per cent			DBE,[b] per cent			Apex-width, cm.		
			Mean	Range	St. dev.	Mean	Range	St. dev.	Mean	Range	St. dev.	Mean	Range	St. dev.	Mean	Range	St. dev.	Mean	Range	St. dev.
42–137	Upl.	Red	11.68	4.2	1.23	4.45	1.9	0.54	4.51	1.9	0.54	5.21	13.73	5.54	1.37	4.3	1.50	1.73	1.4	0.36
42–138	"	"	13.31	3.1	0.96	4.43	1.5	0.35	4.49	1.4	0.35	4.47	9.84	4.22	1.49	4.9	1.55	1.70	0.6	0.17
42–139	"	White	10.07	3.1	0.83	3.78	1.4	0.38	3.83	1.4	0.37	3.72	11.21	4.74	1.23	5.7	1.68	1.90	0.8	0.19
42–140	"	"	10.04	4.9	1.00	4.15	1.7	0.41	4.24	1.6	0.41	7.64	16.88	5.24	2.19	5.1	1.51	2.61	1.3	0.32
42–141	"	Blue	12.31	4.8	1.17	4.67	1.8	0.46	4.76	1.8	0.41	7.29	14.06	4.81	2.06	4.9	1.52	2.08	1.1	0.30
42–142	"	Red	11.84	4.4	1.33	5.47	1.7	0.43	5.78	1.8	0.40	13.77	21.05	4.29	5.68	9.6	2.43	3.34	1.9	0.53
42–143	"	Blue	12.33	5.5	1.68	4.97	2.0	0.59	5.01	1.9	0.60	6.52	14.79	5.36	1.72	5.3	1.59	2.17	2.4	0.56
42–144	"	White	9.89	3.8	1.12	4.21	2.6	0.71	4.25	2.6	0.77	2.83	11.30	4.60	0.92	4.4	1.52	2.22	1.2	0.36
42–145	"	"	8.89	3.0	0.73	3.01	0.6	0.18	3.11	0.8	0.22	10.05	17.98	6.54	3.27	6.9	2.35	1.89	1.2	0.32
42–146	"	Red	11.20	3.3	0.77	3.49	1.2	0.28	3.56	1.3	0.29	6.88	15.24	6.02	2.01	5.7	1.83	1.36	0.7	0.20
42–148	"	"	12.49	5.2	1.38	4.09	1.7	0.48	4.20	1.9	0.51	7.35	17.21	5.19	2.65	6.0	2.01	1.39	1.2	0.33
42–149	"	White	14.49	3.8	1.04	4.33	1.0	0.31	4.38	1.1	0.33	1.18	6.82	2.43	1.05	13.6	3.09	1.21	0.8	0.23
42–150	"	"	10.87	3.2	0.89	4.47	1.1	0.28	4.48	1.0	0.27	0.29	5.56	1.39	0.24	2.6	0.73	2.34	0.9	0.23
42–151	"	"	11.15	4.5	1.23	3.97	2.0	0.58	4.03	1.9	0.57	4.84	17.04	6.50	1.64	6.7	2.34	1.77	1.2	0.30
42–152	"	Blue	13.20	4.5	1.22	4.74	1.2	0.35	4.80	1.3	0.35	4.83	12.75	5.02	1.30	4.3	1.29	1.90	1.5	0.33
42–153	"	White	10.63	3.3	0.79	4.20	1.4	0.43	4.21	1.4	0.42	1.21	10.00	3.03	0.39	2.8	0.94	1.83	1.2	0.29
42–154	"	"	9.91	2.2	0.56	3.81	0.9	0.25	3.88	1.0	0.28	6.34	18.00	6.81	1.85	7.5	2.09	2.06	0.7	0.20
42–155	"	"	9.03	2.5	0.63	3.29	1.0	0.30	3.29	1.0	0.31	0.21	4.21	0.94	0.15	2.9	0.65	1.40	1.0	0.25
42–156	"	Red	12.72	6.1	1.43	4.60	1.7	0.54	4.79	1.8	0.53	10.06	17.78	5.12	4.43	25.0	5.56	2.18	1.0	0.25
42–157	"	"	11.75	3.0	0.93	4.48	1.3	0.40	4.54	1.4	0.42	4.67	21.67	6.49	1.22	5.4	1.72	2.11	1.0	0.28
42–158	"	"	10.32	5.8	1.54	3.82	1.8	0.55	3.91	1.9	0.53	7.72	17.53	6.47	2.38	7.7	2.23	1.72	1.0	0.24
42–158A	"	"	10.65	3.2	0.82	3.24	1.1	0.32	3.28	1.1	0.30	4.04	15.05	6.04	1.31	6.7	1.97	1.44	0.8	0.21
42–159	"	Blue	9.65	2.7	0.63	3.90	0.9	0.24	3.96	1.0	0.24	4.32	12.24	4.29	1.55	5.6	1.59	2.07	0.8	0.21
42–160	"	Red	11.85	3.5	1.00	4.07	1.0	0.29	4.10	1.0	0.31	2.56	11.20	4.12	0.83	4.5	1.37	1.44	1.0	0.26
42–161	"	Blue	10.32	2.6	0.82	3.60	1.4	0.37	3.67	1.5	0.38	6.44	19.57	6.55	1.82	5.1	1.80	1.87	1.0	0.24
42–168	Akal.	Red	10.71	3.4	0.75	4.15	2.0	0.46	4.19	2.0	0.47	3.85	12.62	5.00	0.96	2.7	1.21	2.12	1.2	0.27
42–169	"	"	10.75	4.4	1.11	3.80	1.4	0.37	3.84	1.3	0.38	2.73	11.36	4.15	1.07	4.8	1.57	1.74	1.2	0.29
42–170	"	"	10.78	2.7	0.74	3.58	1.0	0.28	3.69	1.0	0.30	7.68	14.75	4.97	3.10	6.7	2.33	1.79	0.5	0.16
42–171	"	"	12.27	3.7	0.91	4.43	0.7	0.23	4.50	0.9	0.24	4.70	13.49	4.39	1.59	4.8	1.49	1.84	1.2	0.27
42–172	"	"	11.99	5.1	1.23	4.24	1.5	0.43	4.35	1.6	0.44	8.51	15.63	5.16	2.76	7.3	1.94	1.78	0.6	0.18
42–173	"	"	12.61	4.2	1.22	4.83	1.4	0.43	4.86	1.4	0.43	1.37	9.09	2.63	0.53	2.2	0.94	1.39	0.7	0.22
42–174	"	"	8.79	2.5	0.69	3.22	0.8	0.21	3.25	0.8	0.20	3.58	17.07	6.01	0.96	3.4	1.51	1.78	0.8	0.17
42–175	"	"	10.98	2.6	0.82	3.94	1.1	0.27	4.03	1.3	0.29	7.98	15.45	5.19	2.27	5.4	1.61	2.19	0.7	0.18
42–176	"	"	8.51	2.3	0.58	3.12	0.8	0.24	3.18	1.0	0.26	6.60	19.77	7.15	2.08	6.9	2.39	1.76	1.1	0.29
42–177	"	"	9.09	3.1	0.95	3.32	1.2	0.36	3.47	1.3	0.39	9.31	5.53	1.77	4.50	4.4	1.45	1.92	0.8	0.23

[a] DLE, degree of lengthwise eccentricity.
[b] DBE, degree of breadthwise eccentricity.

42–175	"	"	10.98	2.6	0.82	3.94	1.1	0.27	4.03	1.3	0.29	7.98	15.45	5.19	2.27	5.4	1.61	2.19	0.7	0.18
42–176	"	"	8.51	2.3	0.58	3.12	0.8	0.24	3.18	1.0	0.26	6.60	19.77	7.15	2.08	6.9	2.39	1.76	1.1	0.29
42–177	"	"	9.09	3.1	0.95	3.32	1.2	0.36	3.47	1.3	0.39	9.31	5.53	1.77	4.50	4.4	1.45	1.92	0.8	0.23

[a] DLE, degree of lengthwise eccentricity.
[b] DBE, degree of breadthwise eccentricity.

TABLE 3. *The characteristics of the 4 populations.*

Population	No. of sample means	Features																		
		Blade-length, cm.			Midlength-width, cm.			Greatest-width, cm.			DLE,[d] per cent			DBE,[e] per cent			Apex-width, cm.		
		Mean[a]	Range[b]	Stand. error[c]	Mean	Range	Stand. error	Mean	Range	Stand. error	Mean	Range	Stand. error	Mean	Range	Stand. error	Mean	Range	Stand. error
Upland White	10	10.50	5.60	0.50	3.92	1.46	0.15	3.97	1.37	0.15	3.83	9.84	1.06	1.29	3.12	0.31	1.92	1.40	0.13
Upland Blue	5	11.56	3.55	0.67	4.38	1.37	0.26	4.44	1.34	0.26	5.88	2.97	0.56	1.69	0.76	0.13	2.02	0.30	0.06
Upland Red	10	11.78	2.99	0.29	4.21	2.23	0.20	4.32	2.50	0.22	6.67	11.21	1.04	2.34	4.85	0.49	1.84	1.98	0.19
Akalche Red	10	10.65	4.10	0.46	3.86	1.71	0.18	3.94	1.68	0.17	5.63	7.94	0.86	1.98	3.97	0.39	1.83	0.80	0.07

[a] Mean of the sample means.
[b] Range of the sample means.
[c] Standard error of the sample means.
[d] DLE, degree of lengthwise eccentricity.
[e] DBE, degree of breadthwise eccentricity.

TABLE 4. *Characteristics of the population-pairs.*

Population–Pair	Features																	
	Blade-length			Midlength-width			Greatest-width			DLE[d]			DBE[e]			Apex-width		
	D, cm.[a]	E_D, cm.[b]	t[c]	D, cm.	E_D, cm.	t	D, cm.	E_D, cm.	t	D, %	E_D, %	t	D, %	E_D, %	t	D, cm.	E_D, cm.	t
Upland Red–Upland White	1.28	0.58	2.207[f]	0.29	0.25	1.160	0.35	0.27	1.296	2.84	1.48	1.919	1.05	0.58	1.810	0.08	0.23	0.348
Upland Blue–Upland White	1.06	0.84	1.262	0.46	0.30	1.533	0.47	0.30	1.567	2.05	1.20	1.708	0.40	0.34	1.176	0.10	0.14	0.714
Upland Blue–Upland Red	0.22	0.73	0.301	0.17	0.33	0.515	0.12	0.34	0.353	0.79	1.18	0.669	0.65	0.51	1.275	0.18	0.20	0.900
Upland Red–Akalche Red	1.13	0.54	2.092	0.35	0.27	1.296	0.38	0.28	1.357	1.04	1.35	0.770	0.36	0.63	0.571	0.01	0.20	0.050

[a] D = Difference between means of sample means.

[b] E_D = Standard error of the difference between means of sample means.

[c] $t = \dfrac{\text{Difference between means of sample means}}{\text{Standard error of the difference between means of sample means}} = \dfrac{D}{E_D}$.

[d] DLE, degree of lengthwise eccentricity.

[e] DBE, degree of breadthwise eccentricity.

[f] A significant value of t at the 5% level. All other values of t are non-significant at both 5% and 1% levels.

identity of Upland Red and Upland White Populations—in not more than 5 per cent of any sample Population-pairs examined. On the basis of closer correlation with the published *t* values, this difference will occur in about 4 of every 100 sample Population-pairs.

CONCLUSIONS

All differences in midlength-width, greatest-width, DLE, DBE, and apex-width within each of the 4 Population-pairs are too small to be considered significant. All differences in blade-length are non-significant also, except the difference between the Upland Red and the Upland White Populations, which is sufficiently large that it will occur in only 4 of every 100 pairs—assuming identity of the Upland Red and the Upland White Populations. This difference in blade-length means (actually only 1.28 cm., with a range of means among the Upland Red trees from 10.32 to 13.31 cm., and among the Upland White trees from 8.89 to 14.49 cm.) is by itself too small to be of importance to the plant taxonomist, and cannot be used for the practical segregation of taxonomic units.

In conclusion, therefore, further evidence is necessary to determine if the observed differences in leaf Features actually indicate that the Upland White, Upland Red, Upland Blue, and Akalche Red groups are distinct taxonomic Populations. Until that time it may be assumed that the differences are only incidents of sampling from a single normally variable Population, and that the *zapote blanco*, the *zapote colorado* of upland and of akalche, and the *zapote morado*, as occurring in northern British Honduras, are conspecific.

The characterization of the leaves of this entire Population of 35 trees, as expressed by the means, ranges, standard deviations, and standard errors of tables 2 and 3, are estimates of the normal variation of the species. Such statistics can serve as a basis of reference for the future study of variation in normal *Achras* leaves in other parts of tropical America, especially in regard to other Populations that may be thought significantly different.

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SUPPLEMENTARY NOTES ON ARCTIC AND BOREAL SPECIES IN BENSON'S "NORTH AMERICAN RANUNCULI"

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In recent issues of the BULLETIN[1] Dr. Lyman Benson of the University of Arizona has published a noteworthy series of five papers on those members of the genus *Ranunculus* which he recognizes as occurring in North America north of Mexico and including Greenland. From data which I have accumulated during field and herbarium studies extending over a period of more than thirteen years I should like, however, to add the following remarks about the more northerly ranging of these and some related entities. Further details concerning most of them may be found in my "Botany of the Canadian Eastern Arctic, Part I, Pteridophyta and Spermatophyta,"[2] hereafter cited as "Bot. Can. E. Arctic I," or in "Part IV, Subarctic Regions," which now seems unlikely to be completed until after the war.

Had Dr. Benson made it clear in his papers that his "conservatism in assigning ranges . . . is in part a matter of policy" (Benson in lit.), some at least of these notes would have been superfluous; in the absence of any such statement made publicly they are all the more called for. Dr. Benson's "belief that the published range . . . should be based upon the specimens the author has been able to examine himself" (Benson in lit.) is to be commended so long as it does not cramp the subject or seriously derogate the work of others and is moreover the stated reason for ignoring previous authoritative reports. In the absence of such a clear statement of policy the reader will be apt, and rightly, to expect all pertinent material to have been consulted, the previous reports if ignored to have been proved wrong, and the given range in the absence of any admission of doubt to be that known at the time of publication. Any lesser statement may be as misleading as, unfortunately, indiscriminate citation of ranges "from the literature" is liable to be. And so it is with ecological habitats: one cannot rely on obtaining from occasional notes on herbarium labels a true conception of their ranges in the Arctic without knowing what any of those vast and variable regions are really like. Meanwhile it may be noted that I, too, when citing or repeating a report for which I have seen no supporting specimen assume it to be worthy of remark and investigation rather than necessarily correct—unless it is of a "non-critical" plant by a usually reliable, modern author.

[1] Bull. Torrey Club **68**: 157–172; 477–490; 640–659. 1941. **69**: 298–316; 373–386 1942.

[2] Nat. Mus. [Canada] Bull. 92, i–vi, 1–408. 1940.

Dr. Benson's interpretation of many of the taxonomic entities he accepts or disallows is unexpected; but with such matters of opinion, as with inconsistencies in capitalization, for example, I am not at present concerned.

In writing thus I do not intend; where critical, to be so in other than a constructive and purely impersonal manner. Nor do I wish to detract from the value of Dr. Benson's original observations and considered opinions but rather to make them the more usable. To such ends and in an attempt to guard against the repetition of certain errors and misconceptions I offer the following supplementary notes on those species (and a few others) with which my own studies have been concerned: to facilitate reference each species is introduced by a citation of the page on which it is treated by Dr. Benson within the two cited volumes of this journal.

Vol. 68, p. 159. *Ranunculus acris* L. (s.l.) is also widespread in Asia. Whatever its position on the American mainland may be, it appears to be indigenous in Greenland as well as in Iceland (cf. M. P. Porsild, Medd. Grønl. **92**(1): 30. 1932). In Iceland as in Lapland it is to be found high up in the mountains, however little visited these may be. There seems, fortunately, to be no need to change the original (and evidently intentional) Linnaean *acris* to "acer," since the former rendering, although somewhat inelegant, was used as a masculine by Quintus Ennius (239–170 B.C.) and also by Columella and many subsequent "writers of good Latin." Dr. Benson employed the Linnaean *acris* but this has been so frequently changed (particularly of late on the Continent of Europe) that I felt prompted to consult several of Oxford's most eminent classical scholars on the subject; all agreed that Linnaeus's rendering was legitimate and should be retained (see *International Rules of Botanical Nomenclature*, ed. 3, Art. 70, 1935, and cf. p. 142, where "Ranunculus acris" is given as the "Proposed Standard-Species" of the genus).

Vol. 68, p. 649. *R. pedatifidus* J. E. Smith apud Rees, Cyclop. **29**(2) *Ranunculus* No. 72. 1814 (not 1819; see Jour. Bot. **34**: 311. 1896). This is admittedly a bad complex, but, at least in the sense in which it is understood by Dr. Benson (who includes both *R. affinis* R. Br. and "its" var. *leiocarpus* Trautv. among other synonyms), it occurs in Spitsbergen as well as in northern Asia and America (including Greenland), and is thus virtually circumpolar in range (cf. Fernald, Rhodora **36**: 94. 1934; and Bot. Can. E. Arctic I, 221, where additional ecological habitats are described). It has also been found in the Canadian Arctic Archipelago northwards to Harbour Fjord on the south coast of Ellesmere Island (Simmons, Vasc. Pl. Fl. Ellesmereland, 107. 1906), whence specimens are to be seen in the British Museum, Kew, and Copenhagen Herbaria. (Specimens supporting very many of my other statements can readily be seen in the Gray Herbarium of Harvard University or in some other major American institution.) Dr. Benson states that the type material of *R. affinis* came from Melville Island, but this is hardly

allowed for by the range "Yukon to Baffin Island, Labrador . . . ."; nor is it necessarily true, it has seemed to me from a recent perusal of Parry's *Journal* in the light of all available facts (cf. Jour. Bot. **80**: 87. "1942"). Again, "chiefly in the vicinity of Winter Harbour" refers to the *totality* of "Plants observed in Melville Island . . . by the Officers of the Expedition" (R. Brown in Suppl. App. Parry's "Voyage for the Discovery of a North-West Passage, in the years 1819–20," cclxi. 1824); it does not necessarily mean that *R. affinis* was collected at this place, however probable that may seem; nor is it likely that this plant, which is generally uncommon in the Far North, was collected by all of the officers mentioned! The related *R. auricomus* L. and its "var. *glabrata* Lynge" have been reported from East Greenland (Sørensen, Medd. Grønl. **101**(3): 53–4. *pl. 2, 3.* 1933). Concerning this question of whether or not *R. auricomus* occurs in North America, Dr. Benson (in lit.) agrees that although "the older reports were based upon confusion with other species" these of Sørensen may well prove to be correct. According to Britton & Brown (Ill. Fl. ed. 2, **2**: 104. 1913), *Ranunculus auricomus* is the type species of the genus.

Vol. 68, p. 649. *R. Sabinii* R. Br., named after Captain Edward Sabine, and, like *R. affinis,* published in the *Supplement* to the Appendix to Parry's "1st. Voyage," with little doubt occurs also on the mainland coast of North America (Hooker, Fl. Bor.-Am., **1**: 17, 1829; Macoun & Holm, Rep. Can. Arctic Exp. 1913–18, **5**(A): 13. *pl. 5, f. 4.* 1921). It is also *said* to reach the Rocky Mountains (Britton & Brown, Ill. Fl. ed. 2, **2**: 108) and southward to Montana (Davis, Minn. Bot. Studies, II. **4**: 489. 1900, sub nom. *R. pygmaeus* var. *Sabinii*) or Nevada (Simmons, Vasc. Pl. Fl. Ellesmereland, 112. 1906), and has even been reported from the Taimyr Peninsula, Siberia, by Tolmatchew (Compt. Rend. Acad. Sci. U.R.S.S., A, No. 5, 108. 1930). Whether or not these claims can be substantiated it should be noted that according to Simmons (Vasc. Pl. Fl. Ellesmereland, 113. 1906), who has probably observed more *R. Sabinii* in the field than any other botanist, it "prefers the fields of stiff clay." With regard to the above rendering of the specific name, it now appears that the many authors (including myself in Bot. Can. E. Arctic I) who have changed it to "Sabinei" have done so unjustifiably, as Robert Brown's original "Sabinii" was not a "clearly unintentional orthographic error" (*International Rules,* Art. 70) but apparently a form of Latinization which he later repeated (e.g., in *Pleuropogon Sabinii*) and to which many of his contemporaries adhered.

Vol. 68, p. 652. *R. Allenii* Robinson I have recently found as far west as Port Harrison (lat. 58° 26′ N) on the east coast of Hudson Bay. Towards its northern known limits it appears to be confined to grassy or mossy gullies and depressions, or sheltered banks which are likewise deeply invested with snow in winter and remain damp through much of the summer. The relationships of this to the last species and, through it, to the next three listed below

are still in need of elucidation (see Bot. Can. E. Arctic I, 219–20). Even if Robert Brown's actual statement concerning *R. Sabinii* (Suppl. App. Parry's "1st Voyage," cclxiv. 1824) was "Planta inter R. nivalem et pygmaeam media in Herb. D. Sabine exstat" (sic), it seems to me that *R. sulphureus* should be substituted for the former parent if *R. Sabinii* is indeed of hybrid origin.

Vol. 68, p. 656. *R. nivalis* L. In my experience this species is more characteristic of temporarily inundated areas below melting banks of snow and of mossy slopes where there is little competition from herbs of ranker growth than of "Arctic-alpine grassland" which, at least in any form that is familiar and thus termed farther south, is scarcely developed in the Far North. Not only is this term of problematical value, whether it be used for a habitat or for a general zone, but it can be rather misleading when applied to truly arctic regions. In English we should avoid unwarranted Germanisms and write Wolstenholme (not Wohlstenholme), Spitsbergen (not Spitzbergen), etc. In all of the thousands of living examples that I have seen, the fresh flowers of this species were bright yellow, becoming lighter in colour only when faded (contrast Britton & Brown, Ill. Fl. ed. 2, **2**: 107, whose figure is also rather misleading).

Vol. 68, p. 656. *R. sulphureus* Solander apud Phipps, Voy. N. Pole, 202. 1774. Why "perhaps Iceland"—when so many reports of other species have been entirely ignored? I must take the liberty of refuting the contention that this species should be credited to Phipps alone, as the description was contributed by Solander. This is indicated by a MS belonging to the Department of Botany of the British Museum (Solander MSS, vol. 12, genus 2854). According to Mr. J. E. Dandy (in lit.), who was kind enough to make and send me from their war-time place of greater safety a copy of this MS and also of that of *Agrostis algida* (Solander MSS, vol. 3, genus 361), there can be "little doubt that the slips kept by Solander . . . were not part of the MS sent to Phipps but were Solander's own original notes which he kept for his personal use." Thus these notes "contain numerous erasures, alterations, and additions"; to them have later been added the page citations in "*Phipps it.*"; and in the published version there appear further notes on the systematic position of the plants instead of the place of collection, which was evidently considered unnecessary in a work on Spitsbergen. The only other major changes in the published version are in the sequences of words; but Mr. Dandy remarks (in lit.) that "Solander has placed small figures over the words of his MSS which apparently indicate the revised order which, after consideration, he preferred for publication." Thus were the plants of Phipps' "Voyage towards the North Pole," like many others of the day, identified and described not by a ship's captain but by "Linnaeus' favourite pupil" and Banks' assistant Solander, concerning whose MSS Mr. A. J. Wilmott, Deputy Keeper, Department of Botany, British Museum, affirms

(in lit.) that positive knowledge of the relationship between them and the publications to which they gave rise has existed continuously in some quarters. Mr. Wilmott also contends that the case of *R. sulphureus*, like that of *Agrostis algida*, is covered by Art. 48 of the *International Rules* which state that "Where a name and description by one author are published by another author, the word *apud* is used to connect the names of the two authors. . . ." As regards the type locality, this is not Low Island (off the coast of North East Land), but, according to Solander's MS notes, "prope Smierenberg" [in the north-west of the Spitsbergen archipelago, probably on Amsterdam Island; see Lynge, Skr. Norske Vidensk.-Akad. I. Mat.-Nat. Kl. **1938** (6): 7] where, on Phipps's return voyage, a fairly protracted stay was made for scientific work, and where "Dr. Irving climbed up a mountain" (Phipps, Voy. N. Pole, 69). In this exposed region *R. sulphureus* is not infrequent and may be expected to be particularly plentiful in some situations; for, as I have noted in the course of my own travels there, an unusually large proportion of the lowland is occupied by the "boggy tundra" of which, at least in Spitsbergen and the Canadian Eastern Arctic, the present species is far more characteristic than is *R. nivalis* (contrast Benson l.c.).

Vol. 68, p. 657. *R. pygmaeus* Wahlenb. In my material the petioles of the radical leaves, although usually "1–3.5 cm. long," are sometimes 4 or even 5 cm. in length. Again I would emend the "Arctic-alpine grass-land," as this tiny plant in the American Arctic is largely restricted to the little-vegetated inner zones of late-lying snow patches where few other phanerogams persist and where the growing-season is so short that grasses, if any occur, are usually of insignificant development and fail to flower (apart from the diminutive "*Agrostis algida*" Solander apud Phipps). Farther south such habitats, and in them frequently *R. pygmaeus*, are found chiefly at rather high altitudes, e.g., in southwestern Greenland and in Iceland and northern Lapland. Neither in any of these places nor in far northern Canada or Spitsbergen have I ever seen the "pigmy buttercup" inhabiting "meadows"; it is remarkably intolerant of competition from larger plants, and, even in the Arctic, almost all vascular plants and many cryptogams are larger than it! In a recent paper (Am. Jour. Bot. **29**: 498. 1942) Dr. Benson has recorded *R. pygmaeus* var. *petiolulatus* Fernald and *R. verticellatus* Eastwood as confined, or nearly confined, to "Arctic Tundra" (as opposed to "Alphine Tundra" [sic] or other of his "subdivisions"). However, in proposing the variety Professor Fernald (Rhodora **19**: 138. 1917) expressly contrasted it with "typical *R. pygmaeus* of the Arctic regions, Labrador and the Canadian Rocky Mountains," while recently (Bull. Torrey Club **68**: 658) Dr. Benson indicated that this "var. *petiolulatis* Fern." (sic) was still known only from Mt. Albert, Gaspé County, Quebec: so evidently it ought to be excluded from the known flora of the Arctic. Somewhat similar remarks probably apply, though with less force, to *R. verticellatus* Eastwood; for Nome City (which is

not "at Cape Nome"), whence came the only known material of it (see Benson, Bull. Torrey Club **68**: 659), can scarcely be accepted as truly arctic. On the other hand, it would seem desirable to include in the flora of the truly arctic regions *R. kamchaticus* DC. and *R. Camissonis*[3] Schlecht. (or, perhaps more elegantly, Schlechtend., not the misleading "Schleet"; Benson, Bull. Torrey Club **69**: 378–9, and cf. Am. Jour. Bot. **29**: 499); the former species reaches Port Clarence and the Teller Reindeer (not "Ranger") Station (cf. A. E. Porsild, Rhodora **41**: 165, 228. 1939) and the latter species is known from St. Lawrence Bay on the Siberian side and Cape Prince of Wales on the Alaskan side of Bering Strait, as well as from Little Diomede Island between these two stations (A. E. Porsild, Trans. Roy. Soc. Canada III. Sect. 5, **32**: 30. 1938).

Vol. 69, p. 306. *R. Flammula* L. var. *filiformis* (Michx.) Hook. (*R. reptans* L.). I should have preferred to have followed Linnaeus (Sp. Pl. ed. 1, 549) and most subsequent authors in according this plant specific rank, even if it appears to "run into" *R. Flammula* in some places; otherwise we shall find ourselves, in the interests of consistency as botanical exploration goes on, prompted to unite more and more species which on most counts appear abundantly distinct. Whatever it be called, the present plant is circumboreal and wide-ranging latitudinally but except in Novaya Zemlya (Lynge, Rep. Norwegian Exp. Nov. Zem. 1921, No. 13, 39. 1923) appears to reach only the southern fringe of the Arctic and there to be characteristic not so much of the "marshy ground of" lakes, streams, and ditches as of their actual beds, whether or not these dry out in summer (cf. Lynge l.c.).

Vol. 69, p. 311. *R. hyperboreus* Rottb. The "Island of Grønland" is not only misquoted but seriously misleading. This species reaches all the major (and probably most minor) land-masses of the high-arctic regions and "varies greatly with the habitat, having long, trailing internodes and petioles when growing in water—in which case the leaves generally expand and float on the surface, so constituting in the Far North the only 'floating leaf' type. On dry land the whole plant is much condensed, rarely rising more than a few centimetres above the surface of the ground, and having short internodes and much smaller leaves" (Bot. Can. E. Arctic I, 211–213). The species is almost as common in pools or creeping on wet mud in the mountains as on "marshy ground . . . near the sea"; it is hardly a plant of "grassland," even where this is to be found in the Arctic. The var. *Turquetilianus* of my Bot. Can. E. Arctic I, 211, *pl. 6*, from the west coast of Hudson Bay, appears worthy of some mention.

Vol. 69, p. 312. *R. sceleratus* L. Also in Asia. Scarcely arctic or normally even subarctic, but not uncommon in freshwater pools at and around Churchill, lat. 58° 46′ N on the west coast of Hudson Bay. Most individuals

[3] The original spelling and apparently an intentional form of Latinization; *cf. R. Sabinii* (above) and see Schlechtendal, Animadv. Bot. Ranunc. Cand. 1: 12, 30. 1819.

there grow from 20 to 30 cm. high and appear to belong to the typical form, but one collection which I made during my first visit to Churchill in 1934 has the leaf-characters of var. *multifidus* Nutt.

Vol. 69, p. 313. *R. Gmelini*[4] DC. var. *terrestris* (Ledeb.) L. Benson (*R. Purshii* Richardson *op. cit.*, p. 741; not "Richards," "751"). Members of this complex of course occur outside of North America. The present one indeed persists, as Dr. Benson implies, well north in the West (cf. also Raup, Jour. Arnold Arb. **17**: 254. 1936); at Churchill it is plentiful, growing luxuriantly and flowering and fruiting abundantly, while it also occurs somewhat farther north on the west coast of Hudson Bay, near the mouth of Seal River; see specimens in the New York State College of Agriculture at Cornell University and in the Herbarium of the Academy of Natural Sciences of Philadelphia.

Vol. 69, p. 314. *R. Gmelini* var. *yukonensis* (Britt.) L. Benson is given as "northern coniferous forest" and later affirmed (Am. Jour. Bot. **29**: 499. 1942) as there "endemic or nearly so." According to Mr. A. E. Porsild (Rhodora **41**: 229. 1939, sub nom. *R. Purshii* subsp. *yukonensis*), however, it would appear to extend far beyond the ill-defined limits of this "subdivision" of Dr. Benson's "circumboreal flora."

Vol. 69, p. 375. *R. Cymbalaria* Pursh. Plentiful on the west coast of Hudson Bay around Churchill, and long known from West Greenland; forms belonging to its complex occur also in Scandinavia and, according to Hultén (Hist. Arctic & Boreal Biota, 103. 1937), in South America.

Vol. 69, p. 379. *R. glacialis* L. The rather numerous claims of this species from arctic Canada are apparently all without foundation (cf. Bot. Can. E. Arctic I, 215–8). It is unknown from West Greenland, although widespread on the east coast (cf. *R. auricomus* above).

Vol. 69, p. 381. *R. aquatilis* L. var. *capillaceus* (Thuill.) DC. (*R. trichophyllus* Chaix apud Vill.). At least in the sense in which it is upheld by Dr. Benson (i.e., as including *R. subrigidus* W. B. Drew), this is plentiful and grows luxuriantly at Churchill on the west coast of Hudson Bay; some of my material from there was verified by Dr. Drew himself as belonging to *R. subrigidus*. Quite possibly referable here, too, are some of the representatives of the complex that occur in West Greenland (see below); others inhabit the southern hemisphere.

Vol. 69, p. 383. *R. aquatilis* var. *eradicatus* Laestad. (*R. trichophyllus* var. *eradicatus* [Laestad.] W. B. Drew). Also found in shallow eddies in streams. Persists far north of the line indicated by "Quebec to Labrador and Newfoundland" and also well north of any zone of extensive consolidated "grassland." So variable in S. W. Greenland that I am still uneasy about my disposition of some of the forms that I collected in the Julianehaab dis-

[4] The original spelling, which in this instance must be retained; see *International Rules* (as opposed to *recommendations*).

trict in 1937; meanwhile it should be noted that, from farther north in West Greenland, Dr. M. P. Porsild (Medd. Grønl. **58**: 77. 1920) has "with some hesitation" claimed *R. divaricatus* Schrank, whose synonymy suggests that the plant in question may well have been *R. aquatilis* var. *capillaceus* (*R. trichophyllus* var. *typicus* W. B. Drew, Rhodora **38**: 18. 1936), which is at least approached in the Julianehaab district (see above and in Jour. Linn. Soc. **52**: 385. 1943).

Vol. 69, p. 385. *R. Pallasii* Schlecht. This peculiar plant occurs also in the Canadian Arctic Archipelago (about 8 miles inland of Lake Harbour, Baffin Island; see Bot. Can. E. Arctic I, 210–211). Long known from Spitsbergen, Novaya Zemlya, and continental Eurasia; possibly circumpolar.

Vol. 69, p. 385. *R. lapponicus* L. Also known from several parts of Baffin Island in the Canadian Arctic Archipelago (see Bot. Can. E. Arctic I, 214).

While I feel with Dr. Benson (cf. also Am. Jour. Bot. **27**: 807. 1940) that these last two species are so distinctive as almost to demand erection as monotypic subgenera, I cannot help recalling that, at least in Spitsbergen, they appear to hybridize rather freely; cf. also Resvoll-Holmsen, *Svalbards Flora*, 40 (1927). However, we do not necessarily "lump" those genera of grasses, for instance, which are inter-fertile! With regard to the charming and appropriate name *Coptidium*, it seems clear that this should in the first instance be credited to Beurling (or, in view of the Amsterdam Congress changes in the *International Rules*, perhaps to Beurling ex Nyman) instead of to Nyman, though Dr. Benson (l.c.) may well be right in claiming it as his own (positive) *subgenus*. Thus Nyman already cited Beurling ("V. *Coptidium* (Beurl.) . . . C. ranunculoides Beurl.") in his Consp. Fl. Eur. **1**: 13 (1878), and this inadequate citation presumably had reference to Beurling's much earlier but frequently overlooked "Plantae vasculares seu cotyledoneae scandinaviae. . . ." 1–69 (1859), on page 1 of which the name occurs twice. The first time it is used as a sectional (or subgeneric?) name immediately following the generic heading, as follows: "Ranunculus Linn. a. ? Coptidium. 1. R. lapponicus Linn." This is followed by "b. Eurananculus.," there being only the one species under *Coptidium*. The query apparently expressed the author's uncertainty as to whether *Coptidium* should not be upheld as a separate genus, or as a subdivision under *Coptis*, for the second occurrence of the name in this publication is as a generic one in a footnote (no. 10) following the "R. lapponicus Linn." quoted above. This footnote reads as follows: "*Ranunculis* socius invitus, familiarior *Coptidi.* Coptidium ranunculoides Beurl. in herbar. propr." (cf. Nyman, Consp. Fl. Eur. **1**: 13, but contrast Ind. Kew. **1**: 611).

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BULLETIN OF THE TORREY BOTANICAL CLUB
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A REPLY TO DR. POLUNIN

LYMAN BENSON

Dr. Nicholas Polunin's article entitled "Supplementary notes on Arctic and boreal species in Benson's 'North American Ranunculi' " is concerned primarily with habitat notes and range extensions based in part upon field studies in the eastern Canadian Arctic but largely upon published notes concerning the occurrence of species and varieties. He criticizes my work chiefly because I have not relied upon such notes and particularly upon those in his "Botany of the Canadian Eastern Arctic" in determining the ranges of species. However, he admits at the close of the introduction, ". . . I, too, when citing or repeating a report for which I have seen no supporting specimen assume it to be worthy of remark and investigation rather than necessarily correct. . . ."

My conservatism in assigning ranges not only to Arctic species but to all others is a matter of basic policy. It is my belief that in such papers as these the published range of a species or a variety, unless occasionally noted otherwise, should be based upon the specimens or living plants the author has been able to examine himself. Examples are as follows:

1. R. PEDATIFIDUS J. E. Smith. Exact definition of this species is still a puzzle, and I should not attempt it without seeing more Old World material (practically impossible at present). Some of the Asiatic material I have seen indicates great variability, and I have seen only enough to convince myself that the group needs study. My conservatism in assigning it a range reflects caution in dealing with an entity or group of entities in need of better definition, and it accounts for omitting Spitzbergen, since I have seen no material from there. In short, I have given only the range I know to apply to what I have believed to be *R. pedatifidus*, and I have taken no chance on confusion with other types.

2. R. SABINII R. Br. Despite the note in Britton & Brown's *Illustrated Flora* (cited by Polunin) to the effect that *R. Sabinii* occurs in the Rocky Mountains, I know of no reason to believe that it does. Of course, it is possible that, in reorganizing the *Ranunculi* at the New York Botanical Garden while I was there on a fellowship in the summer of 1935, I overlooked the specimens Britton had in mind or overlooked recording them. Many *Ranunculi* which do not occur there have been reported from the Rocky Mountains, and, as a matter of fact, allowing northern species an extension into the Rockies is much more common than the facts would warrant, despite the relationship of the boreal flora to that of the Rocky Mountain System (cf. L. Benson, Am. Jour. Bot. **29**: 494. 1942). Davis' monograph of the North

American *Ranunculi*, published in 1900 and cited by Polunin to the effect that *R. Sabinii* occurs in Montana, seems to be largely a compilation. The chances of the plant's occurring in Nevada may be one in a hundred, at most.

3. R. AURICOMUS has been reported a number of times to occur in North America, but the older reports were based upon confusion with other species. I see no reason why the plant should not be found to occur in Iceland or Greenland, and I have no reason to question Sørensen's identification of his specimens, but still I do not believe I should accept such reports without seeing the specimens myself. This does not reflect in any way upon the authors of the many notes I have come across in the literature, for in numerous cases, which I have been able to investigate, the notes are correct. However, the genus *Ranunculus* is a difficult one, and my interpretation of many entities is new. Consequently, I have not felt it advisable to accept anyone else's interpretation of a plant as being necessarily identical with my own. The result in many cases is understatement of the actual range of a species despite published notes to the contrary. A study of the confusion of names on specimens of *Ranunculus* in practically any large herbarium should be adequate to show the necessity for this policy. Except in a few especially well kept local or regional herbaria, the number of names in agreement with those I have selected is probably less than 35 per cent, although many of the names actually used are synonyms. The confusion of plants reported in the literature is not so great, but experience has shown it to be considerable.

4. R. CYMBALARIA Pursh. According to Polunin ". . . long known from West Greenland; forms belonging to its complex occur also in Scandinavia and, according to Hultén . . ., in South America." The folly of adding this sort of a synthetic range to *R. Cymbalaria* should be obvious from the following: (1) The type occurring in West Greenland is most likely to be not typical *R. Cymbalaria* at all but the var. *alpina*. (2) I have seen no specimens from Scandinavia, but the fact that they belong to the same complex as *R. Cymbalaria* is neither here nor there. In my personal herbarium and elsewhere there are numerous collections of members of the complex from Tibet, the Himalaya Mountains, and western China, but none of these is typical *R. Cymbalaria*, and some seem to represent a separate species while others seem to be between the typical variety and var. *alpina* in many ways but with characters of their own. The Scandinavian plants may be more closely related to these Asiatic ones than to *R. Cymbalaria* or different from either. (3) The South American plant is *R. tridentatus* H. B. K., distinctly different in the specimens I have seen from *R. Cymbalaria*, but related to it.

In the discussions of *R. nivalis* and *R. pygmaeus* and elsewhere, Dr. Polunin takes exception to the term "Arctic-alpine grassland." It is to be noted that I have abandoned it already (Am. Jour. Bot. **29**: 494. 1942), and in view of this I did not suppose he would wish to bother with further dis-

cussion. The references to vegetation types appearing in the articles in this BULLETIN are either the divisions recognized by Shantz and Zon (Natural Vegetation. Atlas of American Agriculture. U. S. Dept. Agr. 1924), or slight modifications of them. Shantz and Zon dealt only with the United States, and "Arctic-alpine grassland" is merely an extension of their term "Alpine grassland." I agree with Doctor Polunin that the term is inapplicable. On the other hand, I am not wholly certain that "Arctic tundra and grassland" would not be a better term than "Arctic tundra," the term I have adopted more recently. Use of the term "tundra" in the more recent publication is an adaptation from Weaver and Clements (Plant Ecology. ed. 2. 1938). As it is used here "Arctic" does not mean about the Arctic Sea or within the Arctic Circle. It refers to a broad vegetational area. Dr. Polunin has overlooked the fact that whatever term may be employed is adopted to refer to the general region above or beyond timber line and the meadows about timber line and not to the habitat of the specific plant. As an example from another vegetation type, a particular species occurring in the western United States may grow in some places among quaking aspens, yet we might designate it as a plant characteristic of yellow pine forests as opposed to sagebrush desert, juniper-pinyon woodland, or oak woodland. This is because in many parts of the West the quaking aspen occurs largely in wet places surrounded by drier forests of *Pinus ponderosa;* in other words, although it may occur in pure stands, quaking aspen does not form a major vegetation type but merely indicates a local condition within a general type. My use of the term alpine tundra refers to the areas above timber line in the mountains of the Far West. *So far as Ranunculus is concerned,* the species occurring in the alpine areas of the northeastern United States and adjacent Canada are with those occurring beyond timber line to the northward. For this reason the areas in the Northeast are lumped with those of the far north, despite the fact that other elements of their included vegetation are not all in agreement with *Ranunculus.*

At various points (e.g. under *R. Allenii* and *R. hyperboreus*) Dr. Polunin bases criticisms upon matters quoted from the original statements of distribution of species and offered by the writer merely as material of possible help in determining the type collections. That under *R. hyperboreus* the data following the heading "type collection" should be taken as a statement of the known distribution of the species at present and criticized as misleading and inadequate and that in the discussion of *R. Sabinii* (under *R. Allenii*) similar data should be taken apparently as an argument concerning the hybrid origin of the species makes refutation of such points unnecessary.

It is with a feeling of disappointment that I find Dr. Polunin's valuable and long-continued observations on *Ranunculus* in the Arctic appearing

merely as a list of supplementary notes correlated with a review of my personal errors, such as accidental misstatement of a title, overlooking of two commas replacing periods after abbreviations, insertion of an unnecessary h in Wolstenholme, and omission of the newly published *R. hyperboreus* var. *Turquetilianus* Polunin because my note to the editor arrived too late to be inserted. Naturally I regret these errors, but I regret still more finding them used in an article in such a way as to overshadow the original observations of an eminent explorer and author.

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RESPONSE OF PYTHIOMORPHA GONAPODYIDES TO MANGANESE

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In experiments in this laboratory on the nutrition of fungi extensive use has been made of a medium containing magnesium sulfate, potassium dihydrogen phosphate, dextrose, and asparagine. This medium was used by Schopfer in his studies on *Phycomyces* (3), and in it *Phycomyces* grows quite satisfactorily if the chemicals used are of the customary C.P. grade. We have assumed that iron, zinc, manganese, and other supplementary mineral elements were furnished by the traces present as contaminants in the constituents of the nutrient solution. However, in most of our experiments we have added to the original medium a mixture of mineral supplements in order to insure their presence.

Although *Phycomyces* grows well in the unsupplemented medium we experienced difficulty in cultivating *Pythiomorpha gonapodyides* unless the mineral supplements were added. This difference in the response of two species of fungi indicated by our preliminary observations seemed worthy of further investigation. The results presented in this paper show that *Pythiomorpha gonapodyides* is especially sensitive to a lack of manganese.

MATERIALS AND METHODS

The fungi used were *Pythiomorpha gonapodyides, Phycomyces blakesleeanus* (+), and *Aspergillus niger*. The first two organisms have complete deficiencies for thiamine. *Phycomyces* grows if furnished the pyrimidine and thiazole intermediates of thiamine; *Pythiomorpha* is able to synthesize the thiazole portion of the thiamine molecule, but must be supplied with the pyrimidine half (1, 2). *Aspergillus* is autotrophic as far as thiamine is concerned.

All three fungi were grown at 25° C in 125-ml. Erlenmeyer flasks each containing 25 ml. of a basal liquid medium. The basal solution contained per liter, 1.5 g. KH_2PO_4 Sorensen (Mallinckrodt A.R.), 0.5 g. $MgSO_4 \cdot 7H_2O$ (Mallinckrodt A.R.), 50.0 g. dextrose (Corn Products Co. C.P.), 2.0 g. asparagine and 400 mμ moles of thiamine (Merck synthetic). The asparagine was purified by treatment with norit A and recrystallization from alcohol. The mixture of mineral supplements used was prepared by adding to 100 ml. of distilled water 5.7 mg H_3BO_3, 15.7 mg. $CuSO_4 \cdot 5H_2O$, 140.4 mg. $Fe(NH_4)_2SO_4 \cdot 6H_2O$, 10.8 mg. $Ga_2(SO_4)_3 \cdot 18H_2O$, 8.1 mg. $MnSO_4 \cdot 4H_2O$, 3.6 mg. acid molybdic 85%, and 79.0 mg. $ZnSO_4 \cdot 7H_2O$. The addition of 0.5 ml.

of this mixture [1] per liter of solution gave the following trace elements in p.p.m.: 0.005 B, 0.02 Cu, 0.10 Fe, 0.01 Ga, 0.01 Mn, 0.01 Mo, and 0.09 Zn. These quantities are later referred to as 1x supplements; twice these quantities, as 2x supplements, and one-fifth, as 0.2x supplements.

Bits of mycelium were used in inoculating cultures of *Pythiomorpha*. In the early experiments irregularities were observed which were traced to differences in the viability of the inoculum. For example, mycelium removed from the center of a colony frequently failed to grow. After some trials it was found that uniform results were obtained when the inoculum was taken from the edge of a colony 2 or 3 days old, grown in a liquid medium. Some further refinements in inoculation are given in connection with the individual experiments.

Dry weights were obtained by drying at 100° C after filtering the mycelium into Gooch crucibles and washing with distilled water, or by washing the mycelium with two changes of distilled water, pressing dry with the fingers and drying in aluminum pans.

All glassware was Pyrex. It was cleaned with chromic-sulfuric acid cleaning mixture, thoroughly rinsed with tap water and distilled water, and drained dry. The solutions were sterilized by autoclaving at 13 lbs. pressure for 25 minutes.

EXPERIMENTAL RESULTS

The Effect of Mineral Supplements on P. gonapodyides. In a preliminary experiment various amounts of the mineral supplements were added to the basal medium. The cultures were inoculated from a four-day-old culture grown in the basal medium plus 2x supplements. The pieces of inoculum were relatively large and no effort was made to remove the culture fluid retained by the mycelium used as inoculum. Dry weights of quintuplicate cultures were determined after 8 days growth (table 1). It appeared that the 1x amount of supplements was superior to the larger or smaller amounts.

TABLE 1. *Average dry weight (5 cultures) of P. gonapodyides grown 8 days in the solutions indicated.*
Growth in the basal solution was the result of transfer of mineral supplements with inoculum. Compare with table 2.

Addition to basal solution	Av. dry wt. in mg.
No addition	30.0
0.2x supplements	41.0
1x supplements	79.3
2x supplements	44.3

[1] The mixture of mineral supplements is based on the work of Steinberg (4) with *Aspergillus niger*. Although boron has not been demonstrated to be required by the fungi it was added because of its essential character for higher plants.

However, greater growth occurred in the basal solution than was anticipated from earlier observations. This was because of the mineral supplements carried over in the inoculum, as was demonstrated by the lack of growth in the basal solution when special precautions were used to minimize the carry over. For example, *Pythiomorpha* was grown in the basal solution, and in the same solution plus 1x supplements. The basal solution was inoculated from cultures 3 days old grown in the basal solution. The solutions containing supplements were inoculated from cultures 3 days old grown in the basal solution plus 2x supplements. Pieces of inoculum were used about 2 mm. in diameter. These were taken from the edge of the colony and each piece was pressed against the side of the flask before it was transferred, in order to remove as much of the culture fluid as possible. Dry weights of quintuplicate cultures were determined after 48 hours incubation.

Under these conditions very little growth occurred in the basal solution while in the same solution to which the mineral supplements were added

TABLE 2. *Average dry weight (5 cultures) of P. gonapodyides in four successive passages in the solutions given.*
Period of growth in each passage, 48 hours.

Culture medium	Av. dry wt. in mg. in passage			
	1	2	3	4
Basal solution	0.4	0.0	0.8	0.0
Basal solution plus 1x supplements	3.9	7.7	9.9	12.7

the growth was quite satisfactory (table 2, Passage 1). Just before determining the dry weights at the end of the first passage subcultures were made from each of the cultures in the basal solutions to fresh flasks of the same medium. This procedure was followed also for the basal medium plus supplements. The fungus failed to grow in the second passage in the basal medium but produced a greater dry weight in the supplemented medium in the second passage than it did in the first passage. For the third passage in the basal medium inoculum was taken from the cultures of the second passage in the supplemented medium. Again growth in the basal medium was slight, but it was excellent in the basal medium plus supplements. An attempt was made to subculture the growth of the third passage in the basal medium without success, while a further increase in dry weight was obtained in the fourth passage in the supplemented medium (table 2).

This experiment, and others of the same character, demonstrated that *P. gonapodyides* would not grow in the basal medium prepared with chemicals of the purity customarily used in our laboratory provided suitable precautions were used to minimize the amount of the supplementary mineral elements carried over from the old to the new solutions in making inoculations.

The addition of a mixture of mineral supplements to the basal solution allowed growth to occur. Which of the elements in the mixture of elements was responsible for this effect?

Influence of Iron, Zinc and Manganese on P. gonapodyides. A deficiency of iron or of zinc was suspected to be responsible for the failure of *P. gonapodyides* to grow in the basal solution. Preliminary experiments showed, however, that the addition of iron or of zinc, or of both elements, failed to correct the deficiency. Manganese, however, proved to be decidedly beneficial. The following experiment in which the three elements were used alone, and in various combinations, illustrates these statements.

P. gonapodyides was grown in quintuplicate cultures in the basal medium, in the basal medium plus 1x supplements, plus iron, plus zinc, iron

TABLE 3. *Average dry weights (5 cultures) of P. gonapodyides grown in the solutions indicated for four successive passages.*
Period of growth in each passage, 48 hours.

Additions to basal solution	Av. dry wt. in mg. in passage			
	1	2	3	4
None	0.2	0.0	....	....
1x supplements	6.9	9.0	16.4	6.8
Iron only	0.2	0.0	....	....
Zinc only	0.1	0.0	....	....
Iron and zinc	0.3	0.0	....	....
Manganese only	3.8	6.1	12.3	3.8
Manganese and iron	3.4	5.0	9.6	2.8
Manganese and zinc	6.4	10.0	15.3	10.0
Manganese, zinc and iron	5.4	4.5	6.3	4.7

and zinc, manganese, manganese and iron, manganese and zinc, and iron, zinc, and manganese. The iron, zinc, and manganese were added as they existed in the 1x amount of supplements, that is, at 0.10 p.p.m., 0.09 p.p.m., and 0.01 p.p.m., respectively. The solutions were inoculated from cultures 3 days old grown in the basal solution plus 1x supplements using the precautions previously described to minimize the carry over. Dry weights were determined after 48 hours.

Growth was slight in the basal solution and in the basal solution supplemented with iron, with zinc or with iron and zinc together, and when transfers were made into the same solutions for the second passage no growth occurred in these media (table 3, Passage 1). Good growth developed in the solutions supplemented with manganese. Growth in the solutions supplemented with manganese and zinc was still better and nearly as good as that obtained when the complete mixture of supplements was used. The addition of iron to the solutions fortified with manganese or with manganese

and zinc reduced the growth somewhat, suggesting that the amount of iron used may have been above the optimum for this fungus. The results obtained in the first passage were in the main confirmed in passages 2, 3, and 4 (table 3).

In general our basal solution appeared to lack sufficient manganese for the growth of *P. gonapodyides*. When adequate manganese was supplied the further addition of zinc improved growth materially, but zinc without manganese was ineffective. Manganese and zinc together were about as satisfactory as the complete mixture of supplements. Again, as in the experiment summarized in table 2, growth improved in later passages as compared to that obtained in passage 1.

Optimum Amount of Manganese for P. gonapodyides. The optimum amount of manganese is probably affected by a number of factors; the

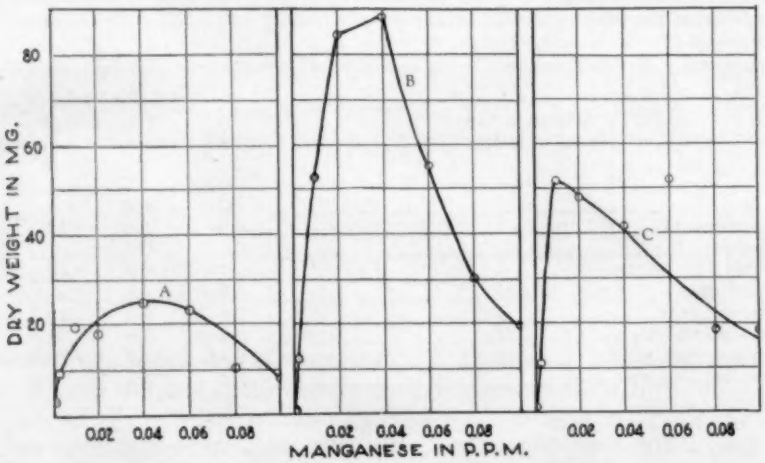

FIG. 1. Average dry weights (5 cultures) of *P. gonapodyides* plotted against the manganese added in p.p.m. to a basal medium. A, passage 2 (3 days growth); B, passage 3 (4 days growth); C, passage 4 (4 days growth).

presence of adequate amounts of zinc in the culture fluid may be important as well as temperature, the character of the inoculum, the time factor, the volume of the nutrient solution and other factors which need not be enumerated here. Although no attempt was made to study the influence of these various factors our results indicate that the optimum addition of manganese to our basal medium probably lies between 0.01 and 0.04 p.p.m. This is illustrated by the following experiment.

P. gonapodyides was grown in quintuplicate cultures in the basal medium and in the same medium plus 0.001, 0.01, 0.02, 0.04, 0.06, 0.08, and 0.1 p.p.m. of manganese added in the form of manganese sulfate. The cultures were inoculated from a culture two days old grown in the basal me-

dium plus 1x supplements. After 3 days of growth subcultures were made from passage 1 into similar media for passage 2. No dry weights were determined for passage 1. After 3 days subcultures were made for passage 3 and dry weights were determined for passage 2. For passage 3 the period of growth was 4 days, and for passage 4 it was 4 days. The results (fig. 1) show some unexplained irregularities, but indicate that with successive passages the optimum range for manganese tends to narrow and to be reduced. It seems probable that for the continued culture of this fungus the addition of 0.01 or 0.02 p.p.m. of manganese to our basal medium would be most favorable.

The quantity of manganese added to a single culture flask amounted to 2.5 μg. for the media containing 0.01 p.p.m. Some growth through 4 successive passages was observed with the addition of 0.001 p.p.m. It is evident that 0.25 μg. of manganese made the difference between failure to grow and continued survival.

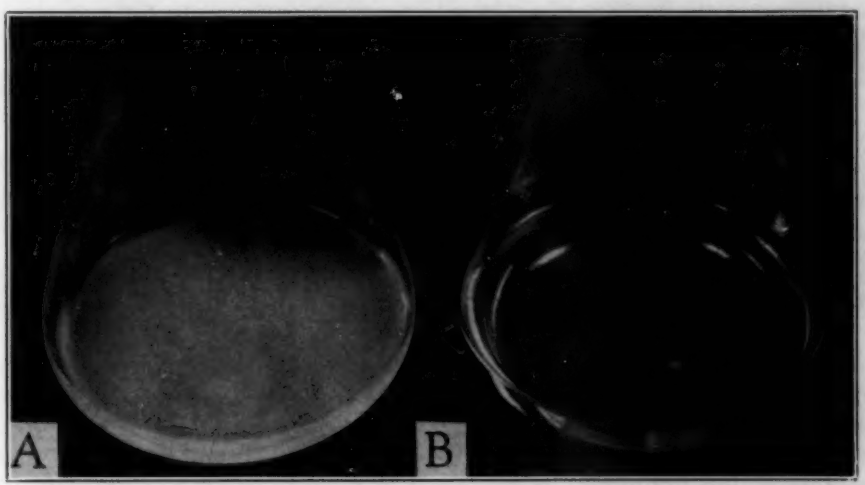

FIG. 2. *Pythiomorpha gonapodyides* growing in a basal solution with no added mineral supplements. A, medium prepared with Baker's analyzed magnesium sulfate; B, medium prepared with Mallinckrodt's magnesium sulfate analytical reagent. Age 5 days.

Presence of Manganese in C.P. Chemicals. In the course of our investigations excellent growth was obtained in one lot of the unsupplemented basal medium. It was found that in the preparation of this particular batch a sample of Baker's magnesium sulfate C.P. had been substituted for the Mallinckrodt magnesium sulfate A.R. which had been previously used. A further investigation demonstrated (fig. 2) that the Baker salt contained sufficient manganese to permit satisfactory growth of *P. gonapodyides*, but the amount in the Mallinckrodt preparation was inadequate. The manufac-

turers' printed labels gave the manganese content of the sample of Baker's magnesium sulfate as 0.002 per cent, of Mallinckrodt's magnesium sulfate as 0.0005 per cent.

Relative Effect of Mineral Supplements on Pythiomorpha, Phycomyces, and Aspergillus. The sensitiveness of *P. gonapodyides* to a deficiency of mineral supplements, especially manganese, suggested that the response of *Phycomyces blakesleeanus* and *Aspergillus niger* also should be determined under our conditions. It was found that both *Phycomyces* and *Aspergillus* grew quite satisfactorily in our basal solution through successive passages. For example, the average dry weights of quintuplicate cultures of *Phycomyces* in 4 successive passages in the basal medium (in which *Pythiomorpha* failed to grow) were as follows: 99.6 mg. (4 days growth), 118.8 mg. (5 days), 140.4 mg. (6 days), and 105.9 mg. (5 days).

TABLE 4. *Average dry weights (4 cultures) of Aspergillus niger, Phycomyces blakesleeanus and Pythiomorpha gonapodyides in the third and fourth passages in a basal medium, and in the same medium plus manganese or a mixture of mineral supplements.*

Period of growth in each passage 5 days.

Addition to basal solution	Av. dry wt. in mg. for *Aspergillus* in passage		*Phycomyces* in passage		*Pythiomorpha* in passage	
	3	4	3	4	3	4
None	80.4	126.5	104.9	117.5	0.0	0.0
0.02 p.p.m. Mn	105.9	169.7	123.1	122.8	44.9	91.3
1x supplements	180.8	216.4	108.1	147.1	48.0	45.8

In another experiment the dry weights of the three fungi were determined in quadruplicate cultures in two passages (3 and 4) in the basal solution, in the basal solution supplemented with 0.02 p.p.m. of manganese, and in the basal solution plus 1x supplements. The period of growth in each passage was 5 days.

The procedure followed in preparing the cultures for which the dry weights are given in table 4 was as follows: A flask of each type of solution was inoculated by a bit of mycelium from a culture 2 days old grown in the basal medium plus 1x supplements. After 4 days subcultures were made from each type of culture medium into similar media. After 3 days growth in passage 2, subcultures were made for passage 3. After 5 days growth subcultures were made for passage 4. Dry weights were determined for passages 3 and 4 after 5 days incubation.

Pythiomorpha failed to grow in the basal solution, but both *Aspergillus* and *Phycomyces* grew quite satisfactorily in that medium through the 4 passages. The addition of the mixture of mineral supplements nearly doubled the growth of *Aspergillus,* made the difference between no growth and

substantial growth for *Pythiomorpha*, and had relatively little effect on *Phycomyces*. Supplementing the basal solution with manganese materially improved the growth of *Aspergillus*, but was not nearly so effective as the complete mixture of supplements; for *Phycomyces* the addition of manganese had relatively little effect; for *Pythiomorpha* manganese was as effective as or more effective than the complete mixture.

DISCUSSION

In considering these results it should be remembered that our basal culture solution contained small amounts of manganese as well as other trace elements. The glassware was Pyrex, not quartz; the distilled water, while of good quality, was not redistilled; the chemicals were not purified by recrystallization or treatment with calcium carbonate. We were not concerned with the absolute necessity of any of the supplemental mineral elements for any of the fungi, but with the question: Why did *P. gonapodyides* fail to grow in a medium in which good growth of *Phycomyces* and *Aspergillus* occurred? It is evident that a deficiency of manganese in the medium was responsible for this result; the quantity of manganese in the basal solution was adequate for *Phycomyces* and *Aspergillus*, but not for *Pythiomorpha*.

Why should *P. gonapodyides* be so much more sensitive to a deficiency of manganese than *Phycomyces* or *Aspergillus*? Several possibilities may be suggested, for none of which we have direct evidence. The difference may be associated with a greater fixation of manganese in an unavailable form by the mycelium of *Pythiomorpha* than by that of either of the other two fungi. Such a situation might require more manganese to saturate the fixation system and supply that needed in metabolism. On the other hand, it is possible that the character of the metabolism differs in the three fungi to such an extent that more manganese is actually needed by *Pythiomorpha* than by *Aspergillus* or *Phycomyces*. The difference would not seem to be related to the solubility or insolubility of manganese in the culture medium. Our basal medium had an initial pH of between 4.5 and 4.7. Both *Aspergillus niger* and *Phycomyces blakesleeanus* increased the acidity of the medium by their growth. *Pythiomorpha*, however, had little effect upon the reaction of the nutrient solution as shown by determinations of the hydrogen-ion concentration in cultures 2, 3, 5, and 7 days old.

Another question which deserves consideration is why the amount of growth of *Pythiomorpha* should change in successive passages in the same supplemented medium. As a rule a marked increase was observed for the first three and sometimes four passages. The differences in the dry weights of *Pythiomorpha* in successive passages were not the result of minor differences in the composition of the solutions used, because all culture media for the successive passages in a particular experiment were aliquots of a

single solution prepared and autoclaved at the beginning of an experiment. A comparable situation was not observed with *Phycomyces* or *Aspergillus*. We assume that by continued cultivation of *Pythiomorpha* in a suitable solution a situation could be reached where the growth would be constant in successive passages; but judging from our results, this would require more than four passages. We might suggest that the phenomenon is associated in some way with the vigor of the inoculum. If so, it would seem further to be related most probably to differences in the activity of one or more enzyme systems, perhaps those with which manganese is associated. This possibility is suggested because the minuteness of the inoculum (a fraction of a milligram in dry weight) from which each culture starts would seem to require the intervention of some catalytic process to produce such differences in dry weight in successive passages as those noted (tables 2, 3).

The inactivity of zinc when used alone, and its beneficial effect in the presence of manganese, is of interest also. This suggests that these two elements play distinct roles in metabolism, a conclusion which follows also from the observations of other investigators that manganese cannot be replaced by zinc. It suggests also that the function in which zinc is active cannot occur until that in which manganese plays its part takes place.

In any event our results show that it is not possible to generalize from the requirements for mineral supplements of one fungus and apply the generalization too closely to others.

SUMMARY

The failure of *Pythiomorpha gonapodyides* to grow in a basal solution composed of magnesium sulfate, potassium dihydrogen phosphate, asparagine, and dextrose of C.P. grade plus synthetic thiamine was due to a lack of manganese. *Phycomyces blakesleeanus* and *Aspergillus niger* grew quite satisfactorily through four successive passages in the basal medium. The addition of zinc and iron, singly or together, to the basal medium did not induce growth in *Pythiomorpha*. Zinc was beneficial in the presence of manganese.

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Literature Cited

1. **Leonian, L. H. & Lilly, V. G.** Studies on the nutrition of fungi. I. Thiamin, its constituents, and the source of nitrogen. Phytopathology **28**: 531–548. 1938.
2. **Robbins, William J. & Kavanagh, Frederick.** Intermediates of vitamin B_1 and growth of *Phycomyces*. Proc. Nat. Acad. **23**: 499–502. 1937.
3. **Schopfer, William H.** Les vitamines cristallisées B comme hormones de croissance chez un microorganisme (*Phycomyces*). Arch. Mikrobiol. **5**: 511–549. 1934.
4. **Steinberg, Robert A.** Growth of fungi in synthetic nutrient solutions. Bot. Rev. **5**: 327–350. 1939.

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THE BEHAVIOR OF EXCISED ROOTS OF HETEROTIC HYBRIDS AND THEIR INBRED PARENTS IN CULTURE

W. GORDON WHALEY AND ALICE L. LONG

In 1941 a series of experiments was begun to study early growth behavior of certain hybrid and inbred strains of tomato and maize. Previous investigations by Ashby (1930, 1932, 1937), Murdoch (1940) and Whaley (1939) had indicated that much could be learned about the phenomenon of heterosis by investigating early post-embryonic growth. In this connection it was thought that cultures of excised roots would be of value since in the first passages they may be expected to show the influence of nutrient materials stored in the seed, and later they present a relatively uncomplicated growth system in conditions that can readily be controlled. Accordingly two sets of cultures were begun, one of tomato and one of maize. Since the techniques employed differed somewhat the data are here presented separately.

TOMATO

The tomatoes used were inbred lines of *Lycopersicon esculentum* kindly furnished by Mrs. Iva M. Burgess of the Maine Agricultural Experiment Station at Orono, Maine. One parent is designated as Red River, the other as Pritchard. Mrs. Burgess (1941) reported considerable hybrid vigor in crosses between these two lines and tests by the authors confirmed her findings. The seeds were sterilized by covering them with 95 per cent alcohol, transferring immediately to a 1 per cent solution of bichloride of mercury for one minute, and then rinsing in several changes of sterile water. It is probable that this treatment was too severe, since it was much less satisfactory than the azo-saline one reported by Robbins (1941). However, enough seeds germinated for purposes of the experiment. Germination was obtained by placing the seeds on a sterile 1 per cent plain agar. The F_1 seeds germinated most rapidly and their roots grew fastest. By proper timing it was possible to obtain the inocula from roots of approximately the same length. Five-millimeter terminal segments were cut with a sterile surgical scalpel from roots about 10 mm. in length. These were transferred to culture flasks. The basal nutrient solution contained per liter 0.333 g. $Ca(NO_3)_2$; 0.063 g. $MgSO_4 \cdot 7H_2O$; 0.063 g. KNO_3; 0.042 g. KC_1; 0.060 g. KH_2PO_4; and 0.0025 g. $Fe_2(SO_4)_3$. All culture solutions contained 2 per cent C.P. cane sugar. For the first passages 0.001 g. of thiamine per liter was added.

TABLE 1. *Average dry weights (mg.) of excised tomato roots grown in solutions supplemented with thiamine.*
Average of 5 roots. Growth period of 45 days for each passage.

	Passage			
	1	2	3	4
Red River	1.3	2.3	2.2	2.6
Pritchard	1.4	1.9	2.0	2.5
F_1	3.3	4.2	4.9	5.4

The roots were grown in 50 ml. of solution in 125-ml. Erlenmeyer flasks kept in diffuse light at 20°–25° C. Sub-cultures were made at 45-day intervals and at the same time each root system (minus a five-millimeter terminal piece removed as inoculum) was carefully washed and dried at 100° C to furnish an index of growth. The amounts of growth attained by each of the lines in the first four passages are given in table 1.

As in the data presented by Robbins (1941) for a cross between Red Current (*Lycopersicon pimpinellifolium*) and Johannesfeuer (*L. esculentum*), the roots of the F_1 which showed hybrid vigor in general vegetative characters, grew consistently more rapidly in the cultures. The increase in growth during successive passages was probably at least partly due to temperature differences. All cultures were within the 5° C range but later passages were grown at the upper end of the range. There may also have been an adjustment period which reduced growth somewhat during the first passage.

At the end of the fourth passage segments were transferred to solutions containing in addition to the thiamine 0.001 g. of pyridoxine and 0.005 g. of nicotinamide per liter. This final transfer was made in two different ways. Those roots designated as Set I in table 2 were subcultured as outlined

TABLE 2. *Average dry weights (mg.) of excised tomato roots grown in solutions supplemented with thiamine, thiamine and pyridoxine, and thiamine, pyridoxine and nicotinamide.*
Growth period 45 days; 5th passage. Average of 5 roots.

	Thiamine	Thiamine Pyridoxine	Thiamine Pyridoxine Nicotinamide
Set I			
Red River	2.9	3.1	5.1
Pritchard	2.6	4.2	4.8
F_1	6.2	10.8	17.4
Set II			
Red River	3.1	3.4	4.9
Pritchard	2.2	5.1	5.6
F_1	6.8	12.7	19.1

above from different roots of the same stock, i.e., each root came from a different seed. Those designated as Set II were obtained by taking the apical segments of the main and lateral branches of the same root. Set II represents root clones while Set I represents different roots of the same genetic stock. Unfortunately the small number of roots used did not permit reliable determination of differences in amount of variation between these two sets.

In both sets the two parents and the hybrid grew better with thiamine and pyridoxine, and still better with thiamine, pyridoxine, and nicotinamide than with thiamine alone. All the hybrid roots grew much more rapidly than those of the inbred parents. Even from so limited an experiment it is possible to draw some conclusions regarding the effects of the different growth substances on the inbred and hybrid lines. Robbins (1941) made a good critical analysis of this question based upon his more extensive data. He found that the roots of one parent (Johannesfeuer) showed a greater response to pyridoxine than those of the other (Red Currant). The roots of Red Currant showed a greater response to nicotinamide than those of Johannesfeuer. The present data seem to suggest that the roots of Pritchard respond better to pyridoxine while those of Red River respond better to nicotinamide. In connection with the fact that the differences here are less distinct than those in Robbins' data it should perhaps be remembered that the two inbred parents in this case are members of the same species, and hence, presumably less genetically different than a line of *L. esculentum* and one of *L. pimpinellifolium*. Robbins found further that when grown in solutions supplemented by all three growth substances one parent (Red Currant) tended to approach the hybrid in amount of growth. In the present experiments neither parent showed an approach to the hybrid with any of the growth-substance supplements used. It is notable in fact, that with thiamine, pyridoxine, and nicotinamide growth of the hybrid roots was increased to almost three times what it was with thiamine alone, while that of each parent was only about twice as great. These data furnish some evidence for Robbins' idea that one of the factors concerned in heterosis may be the ability to synthesize or utilize certain growth substances and that hybrid superiority may be partly due in some instances to ability derived from one parent to synthesize or utilize to better advantage one group of essential substances, and from the other parent ability to synthesize or utilize a different set of essential substances.

MAIZE

Although it was recognized that maize roots are apparently not adapted to comparatively easy culture by the methods so far evolved, as are those of tomato, it was thought that an attempt to culture them might reveal

some data of interest. After several abortive essays a partially successful method was developed. The data contribute nothing toward the solution of how to grow maize roots in culture but they do seem to have some significance for certain aspects of the heterosis problem.

Seeds were sterilized by soaking for two minutes in 95 per cent alcohol and then transferring to a 2 per cent solution of bichloride of mercury for two minutes. The seeds were then washed thoroughly in four changes of sterile water and germinated on moist filter paper in sterile Petri dishes. The roots were allowed to grow until a 10-millimeter segment could be cut from the apex for transfer to the culture solution. It was found that in

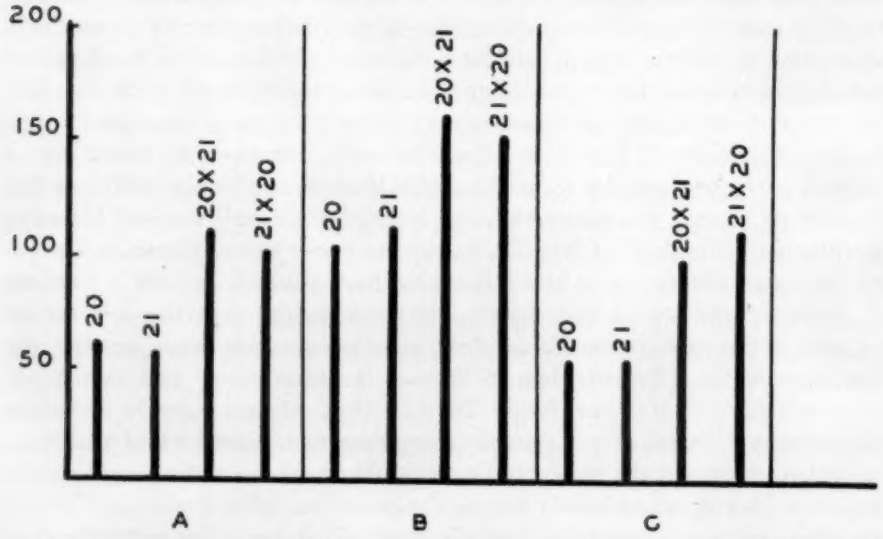

FIG. 1. Average growth (length) of maize roots (lines 20, 21, and hybrids) in solutions supplemented with (A) thiamine, (B) thiamine and pyridoxine, and (C) thiamine, pyridoxine, and nicotinamide. Average of the first six passages, each passage of seven days; average of ten roots per passage.

both crosses used the hybrid seeds germinated much more rapidly. To compensate for this growth difference and for individual variation from seed to seed within a strain, large numbers of seeds were started at predetermined intervals. In this way 10-millimeter segments were all cut from roots of approximately the same length. Eighteen cultures of each strain were started, but measurements were made on only ten; the ten showing greatest growth being selected in each instance. Various basal media were tested, Pfeffer's solution, which was also used in culturing the tomato roots, finally being chosen. Instead of sucrose all solutions contained 1.6 per cent dextrose and were made semi-solid by addition of 5 g. purified agar per liter. (Purification of agar was by the pyridine-ethyl alcohol method out-

lined by Robbins and Ma, 1941.) Growth conditions were the same as those noted above. Subcultures were made at seven-day intervals since it was found that subculturing at frequent intervals resulted in better growth of all the roots. Since roots of the strains used are approximately the same in diameter and since no secondary roots were developed, length was chosen as the simplest measure of growth. Seeds of two crosses were obtained from Dr. D. F. Jones of the Connecticut Agricultural Experiment Station at

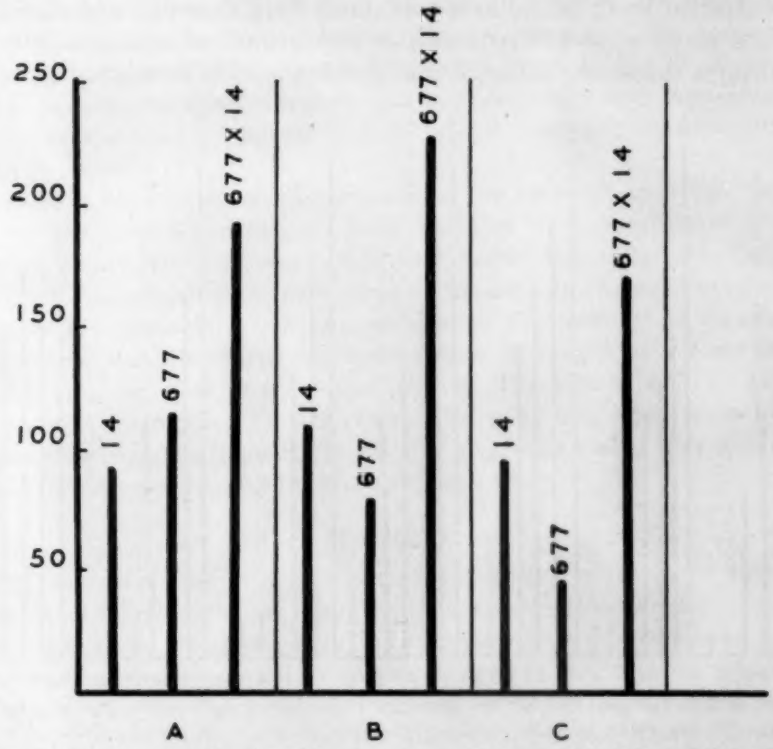

FIG. 2. Average growth (length) of maize roots (lines 14, 677, and hybrids) in solutions supplemented with (A) thiamine, (B) thiamine and pyridoxine, and (C) thiamine, pyridoxine, and nicotinamide. Average of the first six passages, each passage of seven days; average of ten roots per passage.

New Haven. The inbreds and crosses are designated as 20, 21, 20 × 21, 21 × 20, and 677, 14 and 677 × 14, respectively. These crosses showed considerable hybrid vigor under both field and greenhouse conditions.

With these roots culture solutions were augmented from the beginning with thiamine, thiamine and pyridoxine, or thiamine, pyridoxine, and nicotinamide in the amounts of 0.001 g., 0.001 g., and 0.005 g. per liter, respectively. Figures 1 and 2 show average growth of ten roots of each type during the first six passages. To those roots whose growth is repre-

sented in block A thiamine was added; to group B thiamine and pyridoxine; to group C thiamine, pyridoxine, and nicotinamide. In the 20, 21 material the addition of pyridoxine to cultures already containing thiamine caused a marked growth increase in roots of both hybrids and inbreds. This increase appeared to be absolutely, and not relatively, about the same in all strains. The condition would seem to indicate a pyridoxine deficiency in both parental strains and their hybrids. The addition of nicotinamide, in the concentration used, to cultures containing both thiamine and pyridoxine brought about a marked reduction in root growth as compared with that in cultures containing thiamine and pyridoxine. The amount of growth in

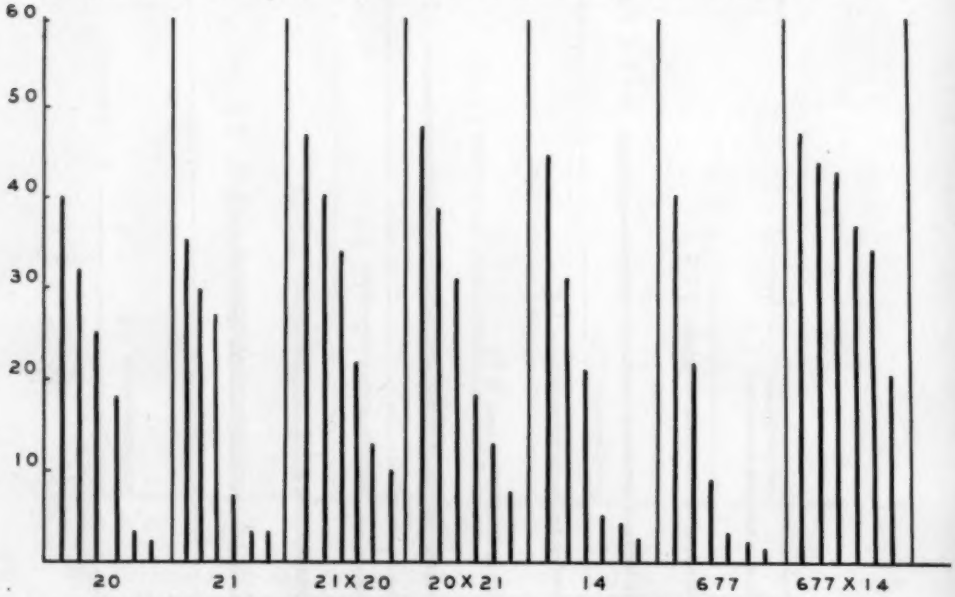

FIG. 3. Average growth (length) of maize roots during each of the first six passages. Average of ten roots in each passage; passages of seven days each. Cultures supplemented with thiamine and pyridoxine.

cultures containing all three substances about equaled that in cultures containing thiamine alone. Further experimentation would be necessary to discover the reason for the inhibition of growth by nicotinamide.

The roots of lines 677 and 14, and the cross 677 × 14 reacted in a somewhat different manner. As in the above experiment the hybrid roots here consistently grew better than those of the inbreds. The actual hybrid advantage above either the average of the parents, or the better parent is higher in this case than in the preceding one. When cultures containing thiamine and pyridoxine were compared with those containing thiamine alone in this case it was seen that the growth of one parent (14) and the hybrid (677 × 14) was increased. The growth of the roots of the other

inbred (677) was decreased. The further addition of nicotinamide again had the effect of limiting growth, but not quite as uniformly as in the previous cross. One inbred (14) was decreased but little, its growth being still greater than with thiamine alone. The other inbred (677) was decreased very markedly, its growth being less than half that with thiamine alone. The hybrid was decreased by about the same amount as in the 20 × 21 cross.

The data seem to indicate that 14 and 677 × 14 are deficient in their ability to synthesize pyridoxine. The significance of the reaction of 677 is not suggested. This inbred line was difficult to handle in all the experiments. Germination was slow, and the percentage very low. Even the best cultures showed a tendency toward lateral branching characteristic of inhibited growth.

Figure 3 shows the average growth of ten roots of each line during each of the first six passages. These cultures were supplemented with thiamine and pyridoxine, since this combination generally gave the best growth. The inadequacy of the method is disclosed by the manner in which the growth diminished from one passage to the next. It is significant, nevertheless, that growth of the hybrid roots decreased to a lesser extent and less rapidly than that of the inbreds. The hybrid 677 × 14 was particularly outstanding in this respect. Roots of this plant made by far the most satisfactory growth. Of all the plants used only this one made satisfactory growth beyond the sixth passage.

DISCUSSION

The use of excised roots permits study of certain metabolic processes under conditions much less complex than those encountered with intact plants. The data presented here indicate that heterosis produces hybrid vigor in small portions of roots grown in culture media under laboratory conditions. This fact is revealing with respect to the physiological mechanism responsible for hybrid vigor. It allows elimination of some factors as being of primary importance in the production of hybrid vigor. Ashby's work (1930, 1932, 1937) indicated that photosynthesis played no part in the hybrid advantage in either maize or tomato. The present data certainly show that hybrid vigor is developed without photosynthesis. (Data to be published subsequently show that photosynthetic differences may increase the relative amount of hybrid vigor.) The gas exchange incident to photosynthesis, and the various translocation factors are also eliminated here. Ashby finally decided upon the size of the meristematic mass within the embryo as the immediate causal agent. He was primarily concerned with the stem apical meristem since this is the source of the bulk of plant tissues. In root cultures the only continuing meristematic mass is the root meristem.

Histological examination of the root tips in the present study revealed no size differences among the different root meristems. The "meristematic mass" influence is therefore ruled out in this case. Nutrient materials derived from the seed are also ruled out for quantitative considerations. The original apical segments were cut from the roots before the available nutrient material in the seeds was exhausted. In intact plants the hybrid might gain an advantage by a longer endosperm nutrition period during the early seedling stage. In the tomato and maize strains tested, hybrid vigor cannot be directly dependent upon this factor. There still remains the possibility of qualitative influence of seed-stored nutrient materials. Certain substances might be more readily available to the hybrid embryos, or be of greater potency. In tomato this seems a very remote possibility in relation to the better growth of the roots in culture. Each root segment was allowed to grow for 45 days before subculturing. In the fifth passage, 180 days from germination of the seed, the roots were still making relatively the same amount of growth as in the first passage. Seemingly any advantage arising from qualitative differences in seed nutrients would have disappeared long before this point was reached. The behavior of the corn roots in culture makes an evaluation of this factor more difficult. The diminution of growth in progressive passages might suggest that some essential substance is derived from the endosperm, and that the original amount diminishes in each passage. That the continued advantage of the hybrids during successive passages depended altogether upon greater availability of this substance seems again unlikely.

The data are best interpreted on the assumption of fundamental metabolic differences between the inbreds and hybrids. In the tomatoes, roots of Pritchard were unable to synthesize pyridoxine in amounts sufficient to permit maximum growth. The roots of Red River had a like deficiency with respect to nicotinamide. Crossing produced hybrids in which the deficiencies of both parents were largely eliminated. The simplest genetic interpretation of this situation is that each parent is homozygous for a deleterious recessive factor—the inability to synthesize or utilize enough of a certain substance or substances. These recessives appear to be at different loci in each parent since crossing masks their effects. This explanation may hold only for the experimental conditions maintained, but that does not affect its validity. Much the same interpretation may be made for the corn root cultures. Here, however, certain of the substances utilized to greater advantage by the hybrid may be derived from within the system, perhaps from the endosperm instead of from the culture media. An exhaustion of such substances may partially account for the progressive diminution of growth in successive passages. It is probable that fundamental physiological differences are to be expected between two such plants.

The differences between the excised hybrid and inbred roots appear then to be fundamental differences in cellular metabolism. These differences in the efficiency of metabolism appear to depend partly, in turn, upon the supply, either internal or external, of certain essential substances.

SUMMARY

Excised roots of tomato and maize were grown in Pfeffer's solution containing separately thiamine; thiamine and pyridoxine; and thiamine, pyridoxine, and nicotinamide. In cultures containing thiamine the roots of one inbred strain of tomato, Pritchard, responded better to the addition of pyridoxine. Those of the other, Red River, responded better to the addition of nicotinamide. The hybrid roots were better than those of either inbred in all culture media.

Excised maize roots showed progressive growth diminution in successive passages in all media. The hybrids showed greater growth in each of six passages, and greater average growth than the inbreds. In cultures containing thiamine the parents and hybrids of one cross, 20, 21, 20 × 21, and 21 × 20, showed increased growth in the presence of pyridoxine, decreased growth in the presence of pyridoxine and nicotinamide in the concentration used. The roots of the other cross reacted in a like manner but less consistently.

It is suggested that the hybrid advantage derived from more efficient metabolism giving the hybrid roots greater ability to synthesize and/or utilize certain essential substances.

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Literature Cited

Ashby, Eric. 1930. Studies in the inheritance of physiological characters. I. A physiological investigation of the nature of hybrid vigour in maize. Ann. Bot. **44**: 457–467.

———. 1932. Studies in the inheritance of physiological characters. II. Further experiments upon the basis of hybrid vigour and upon the inheritance of efficiency index and respiration rate in maize. Ann. Bot. **46**: 1007–1032.

———. 1937. Studies in the inheritance of physiological characters. III. Hybrid vigour in the tomato. I. Manifestations of hybrid vigour from germination to the onset of flowering. Ann. Bot. II. **1**: 11–41.

Burgess, Iva M. 1941. Hybrid vigor in some tomato crosses. Proc. Am. Soc. Hort. Sci. **38**: 570–572.

Murdoch, H. A. 1940. Hybrid vigor in maize embryos. Jour. Hered. **31**: 361–363.

Robbins, W. J. 1941. Growth of excised roots and heterosis in tomato. Am. Jour. Bot. **28**: 216–225.

Robbins, W. J. & Ma, Roberta. 1941. Biotin and the growth of *Fusarium avenaceum*. Bull. Torrey Club **68**: 446–462.

Whaley, W. G. 1939. A developmental analysis of heterosis in *Lycopersicon*. Am. Jour. Bot. **26**: 609–616, 682–690.

———. Heterosis. Bot. Rev. [In press.]

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FLORAL ANATOMY OF SOME SPECIES OF CORNUS

Antoinette Miele Wilkinson

INTRODUCTION

This investigation of the genus *Cornus* is part of a study of members of the Cornaceae, Araliaceae, Caprifoliaceae, and Rubiaceae. The purpose of the study is to discover, if possible, evidence indicative of the fundamental structure of the inferior ovary, and the relation of these families to one another and to other families.

A review of the extensive literature on the nature of the inferior ovary by Miss Gertrude Douglas (6) has appeared in a recent number of the Botanical Review. This literature is also discussed, in part, in MacDaniels' paper (10) on the structure of various pome fruits. However, with respect to the morphology of the Cornaceae, publications are meager and have come primarily from the work of Horne (8), Martel (11), and Baillon (1). These publications will be considered in the discussion.

MATERIAL AND PROCEDURE

So far as possible, living material of buds, flowers, and young fruits was used in the preparation of slides.

Fresh material was killed and fixed in F.A.A. made up with 70 per cent ethyl alcohol (3). After having been washed with 70 per cent ethyl alcohol, the material was placed first in 83 per cent, then in 95 per cent ethyl alcohol. Dehydration was completed by successive immersions for an hour in each of the following mixtures:

95 per cent ethyl alcohol	3 parts	1 part	1 part
Tertiary butyl alcohol	1 part	1 part	3 parts

Several changes in pure tertiary butyl alcohol followed, before the material was gradually infiltrated with paraffin.

Herbarium material was first softened in a solution of 1 per cent NaOH or KOH for 12–24 hours, then washed in running water 12 hours. Dilutions of ethyl alcohol were used to dehydrate, after which dehydration and infiltration proceeded as above.

A rotary microtome was used for sectioning and the sections mounted serially. Miss Jackson's crystal-violet–erythrosin schedule (9) was used with slight modifications. In staining herbarium material, a mordant was necessary to secure adequate differentiation. Before being stained in crystal violet, therefore, the slides were placed in a 1 per cent aqueous solution of chromic acid.

No less than three and an average of five serials of each species, were examined. Because of the anatomical variability found, the actual number of flowers of each species is of interest; these numbers are as follows:

C. florida 4	*C. brachypoda* 4
C. mas 5	*C. glabrata* 3
C. canadensis 4	*C. racemosa* 4
C. suecica 9	*C. stricta* 4
C. controversa 5	*C. alsophila* 5
C. alternifolia 5	*C. rugosa* 5
C. oblonga 3	*C. Amomum* 5
C. Drummondi 5	*C. stolonifera* 8

In all, sixteen species of the genus were sectioned and studied. These comprise a third of the genus, and were selected to represent as many subgroups in the genus as possible. Herbarium sheets of the species are cited.

GENERALIZED FLORAL ANATOMY

In gross morphology, the flower of *Cornus* is 4-merous, generally perfect, and epigynous. The bilocular ovary has a single style, and, pendant from the upper part of the septum, a single anatropous ovule in each locule.

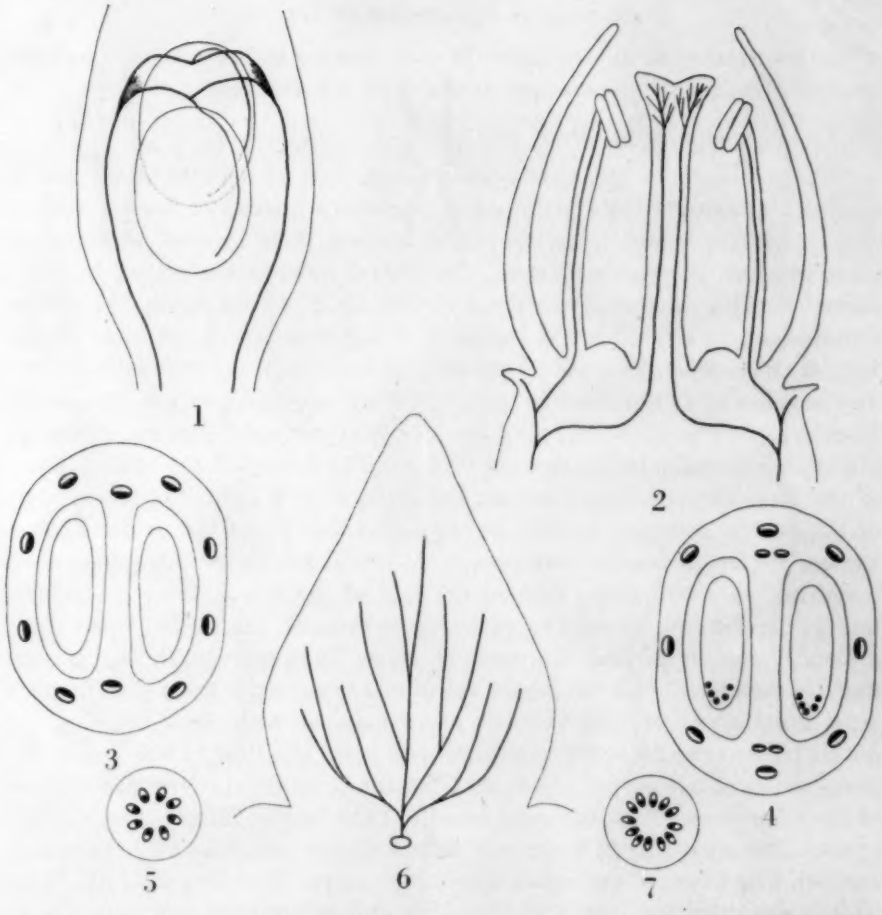
Although the floral anatomy indicates that the essential structure of certain gross features is different from the apparent structure, it does in general substantiate the gross morphology. To minimize repetition, and to establish a basic pattern for the description of the individual species, the floral anatomy of a generalized type is first described. This generalized flower type is characteristic of no particular species, nor is any anatomical feature described necessarily common to all the species studied.

Beginning at the lower part of the receptacle, the vascular tissue is found to consist of a ring of several bundles.[1] These become organized into eight main bundles (fig. 5) which gradually and simultaneously proceed toward the periphery. Usually in the receptacle, but occasionally in the ovary proper, a ventral bundle separates centripetally from each of two opposite bundles. This bundle is composed of a ventral trace of one carpel and the adjacent ventral trace of the second carpel. These always run up in the wall of the ovary, at each end of the septum (fig. 3). Before reaching the region of ovular attachment, the ventral bundles fork radially (fig. 4) and, somewhat above this region, divide into several traces which form an arc

[1] The term bundle is here used in two senses: to mean a vascular cord morphologically composed of several traces, or the strand within the floral member. A trace is the vascular strand supplying an organ from its place of origin (often receptacle) to its entrance into that organ. To illustrate: the ovular bundle is the vascular supply within the ovule; the ovular trace is the vascular strand which runs from the ovule to the ventral bundle; the ventral bundle consists of two ventral traces which are morphologically distinct but often fused and histologically inseparable. See Eames (7) for terminology.

running periclinally in the ovary wall (fig. 13). The outer traces arch and descend in the septum to the region of the funiculus, where each unites with the opposite trace of the corresponding carpel. The bundle resulting from the union enters the ovule (fig. 1). All but one or two of the intermediate branches also arch and descend toward the septum but terminate at various levels and at various distances from the ovary wall (fig. 1). The exceptional traces unite and turn in toward the center, where they enter the style and end in the lower half of the stylar column (not shown in figure 1). Within the ovule, the ovular bundle descends the length of the raphe, branching distally. In the upper part of the ovary, sometimes even above the locule, the dorsal traces separate from two opposite peripheral bundles of the ovary (fig. 2). When they reach the top of the ovary, they extend horizontally toward the style and enter it, continuing to the stigma and branching profusely (fig. 2). In the lower half of the ovary, lateral traces of the carpel separate from the peripheral bundles. These proceed various distances up the ovary wall. Most of them bend centripetally at the top of the ovary and run horizontally: some of these end free; others join the dorsal traces.

The eight main bundles remaining are the peripheral bundles. In the body of the ovary, these have a definite arrangement with respect to the ventral bundles. The bundles with which the ventral bundles are united at the base may still be more or less in the same radii as the ventral bundles (fig. 4); or they may shift periclinally in opposite directions so that they lie in the line of the locule (fig. 3). In either case, the remaining six bundles are accordingly disposed in radial symmetry. Since the change is secondary, and since the arrangement is not constant for a species, it seems of slight importance. Of the eight bundles, four are stamen bundles and the alternating four are petal bundles. Each stamen bundle divides tangentially. Of the two resulting traces, the centrifugal trace is the sepal trace; the centripetal, the stamen trace (fig. 26). The petal bundles, however, divide radially, cutting off a small trace on each side (fig. 26). The middle trace is the petal trace, and each of the lateral traces is a lateral trace of the sepal adjacent. The sepal supply, therefore, consists of the trace centrifugal to the stamen trace, plus the adjacent traces separated radially from the petal bundle on each side of the stamen bundle. In close succession, the sepal traces enter the sepals; the petal traces, the petals; and the stamen traces, the stamens. Within the sepal, the median trace is the strongest, the lateral traces being weak and scarcely entering the calyx lobe. Within the petal, the petal trace forks several times, resulting in a highly vascularized petal (fig. 6). The stamen bundle usually continues single in the filament. Above the departure of the traces to the various floral cycles is a mound-like nectariferous disc which consists of deeply-staining secretory cells (fig. 2). The disc, however, has no vascular supply.



FIGS. 1–7. *Cornus;* Anatomy of the flower. FIG. 1. Ovular and ventral supplies. Ventral traces not bending centripetally in the receptacle; ovular traces arching in the septum, uniting with the opposite ovular trace of the same carpel; intermediate (vestigial) ovular traces also arching but ending in the septum. FIG. 2. Sepal, stamen and dorsal trace derived from a peripheral bundle of the ovary; distal branching of the dorsal bundles in the stigma; mound-like nectariferous disc above the ovary without vascular supply. FIG. 3. Ventral bundle composed of ventral trace of one carpel and the adjacent ventral trace of the second carpel; the ventral bundles are located in the ovary wall at each end of the septum; peripheral bundles with which the ventral bundles are united at the base are not in the same plane as the ventral bundles at this higher level. FIG. 4. Pair of "foreign" ventral traces in the ovary wall at each end of the septum; pair of peripheral bundles with which ventral traces are united at the base are in the same plane as the ventral traces at this higher level—this contrasts with the condition in fig. 3; branching of ovular bundle in the ovule. FIG. 5. Eight main bundles in the receptacle. FIG. 6. Branching of the petal bundle after entering the petal. FIG. 7. *C. florida.* Stele of the receptacle differing from the condition in other species studied (fig. 5), in having numerous strands.

ANATOMICAL DESCRIPTION OF SPECIES

A description of the anatomy of each species follows. If the anatomy resembles that of the generalized flower type, it is omitted.

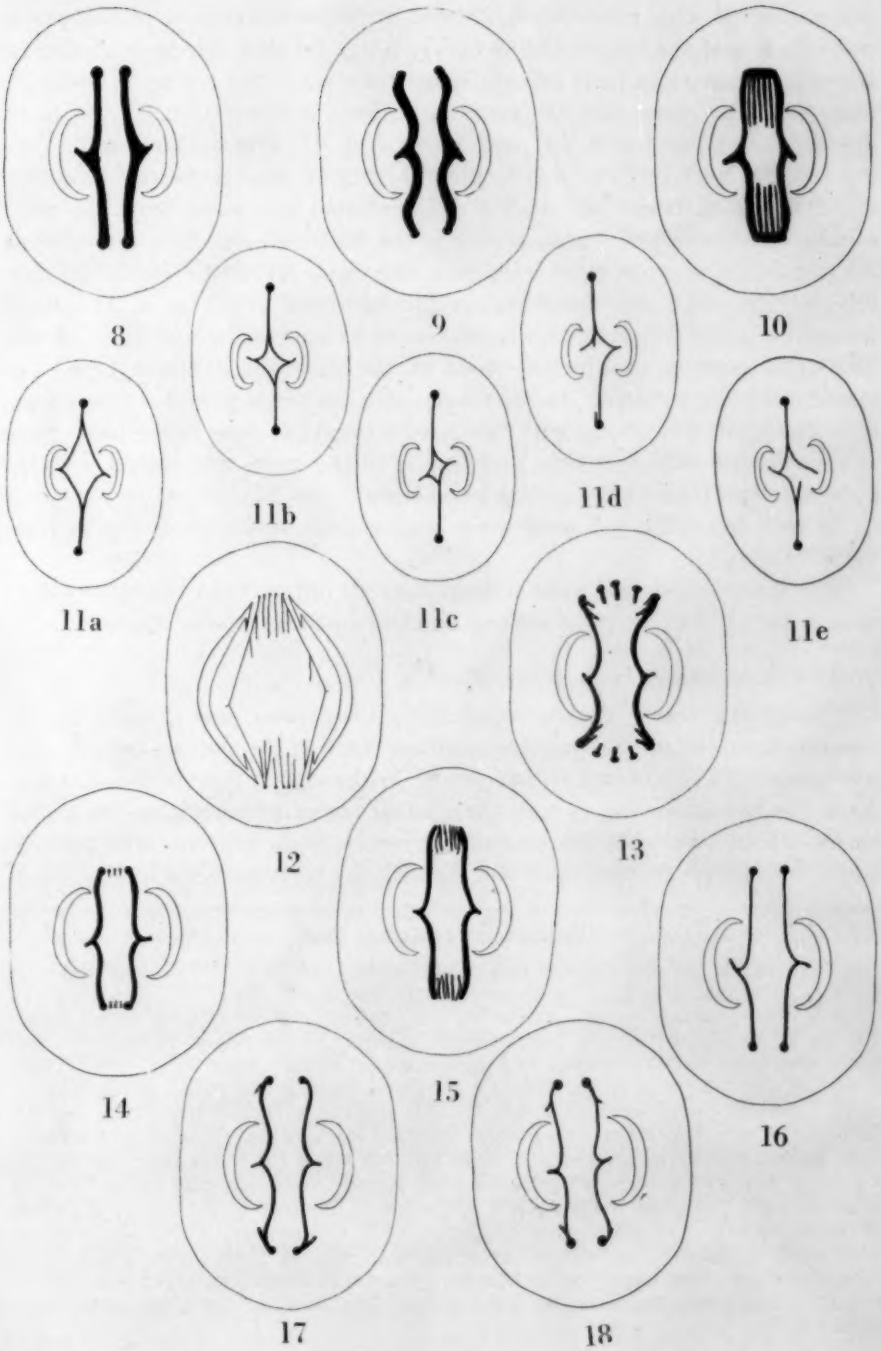
1. C. FLORIDA L. *A. Miele 283* (C).

The receptacle of this species differs from that of the rest of the species studied in having a stele composed of numerous instead of several strands (fig. 7). Nevertheless, as in the other species, these become organized as eight bundles. In some specimens, the ventral bundles are cut off from the stamen bundle, in others from the petal bundle. From its origin, the ventral bundle continues fused to the region of ovular attachment, where it divides into its two component traces. Very shortly, each ventral trace bends inward and becomes an ovular trace to the ovule of its respective carpel. The ovular trace is an extraordinarily heavy one and it arches only slightly, extending almost horizontally in the septum (fig. 8). The fusion of the ovular traces of the same carpel before entering the ovule is very light, for the identity of the pair is apparent as they swing across the top of the ovule. Though the ventral traces usually terminate in the ovular traces, two specimens show a ventral trace continuing beyond the roof of the locule. Here the ventral bundle divides into three: two outer heavy strands, the ovular traces; and a slender middle strand, the ventral trace. In flowers with the ventral bundles associated with the sepals, the dorsal traces arise from the alternate sepal bundles; where the ventrals are associated with petal bundles, the dorsal traces arise from the remaining two petal bundles. In one flower, the dorsal trace of one carpel separates from the petal bundle, the dorsal trace of the other carpel from the sepal bundle. There are no lateral traces in this species. The sepal supply is the most extensive and complex of all the species studied. The bases of the sepals are united into a tube almost 1 mm. long. This is one-third the length of the calyx and is the most extensive fusion found. From both stamen and petal bundles, two traces are cut off radio-tangentially. These traces divide usually twice and the branches ascend in the calyx tube and anastomose somewhat (fig. 21). The species is rather conspicuous in the precocious division of the sepal and stamen bundles. This cleavage often occurs at a level below the roof of the locule; in two stamen bundles the separation occurs half-way down the ovary. The petal supply stands in strong contrast to the sepal supply in having the single petal trace divide into just three branches after entering the petal.

2. C. MAS L. *A. Miele 281* (C).

This species is somewhat intermediate between the preceding species and the pair of "herbaceous" species to follow.

The ventral bundles usually separate rather high in the ovary from the stamen bundle. Though two flowers show one ventral bundle double and


8
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11b
11d
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one single, the usual condition is a fusion of the two unrelated ventral traces more than half the length of the ovary. After forking, the pair of ventral traces move apart in their ascent. When they reach the region of ovule attachment, they turn into the septum, without arching (fig. 9). As in *C. florida*, the ovular traces are very heavy (fig. 9). The ovular bundle does not branch. Surrounding each locule is a ring of large secretory cells (fig. 36). The dorsal traces are weakly differentiated and arise from the petal bundles or stamen bundles according as the ventrals arise from these. Weak differentiation of a few other bundles in one ovary makes it difficult to ascertain whether they are ramifications of the dorsal trace, or weak lateral traces. The sepal supply of this species is not so complex as that of *C. florida*. The petal bundles behave like those of the generalized flower type. The stamen bundles, however, divide tangentially to produce either three separate strands or one strand with two lateral branches close to the base. Each of these lateral branches runs periclinally in the ovary and unites with the adjacent sepal trace of the nearby petal bundle (fig. 23).

Within the petal, the petal trace may remain single or divide to form three strands.

One flower was found to be tricarpellary. It differs from the bicarpellary flowers only in having three ventral bundles and three dorsal traces.

3. C. CANADENSIS L. *A. Miele 285* (C).

The ventral traces, usually separate for the greater part of their length, separate from the stamen bundles relatively high in the ovary—usually near the base of the locule and in one flower in the upper fourth of the ovary. As in the two preceding species the ventral traces terminate in the ovular traces. About level with the roof of the locule, these bundles arch and descend through the septum, each uniting with the corresponding ovular traces

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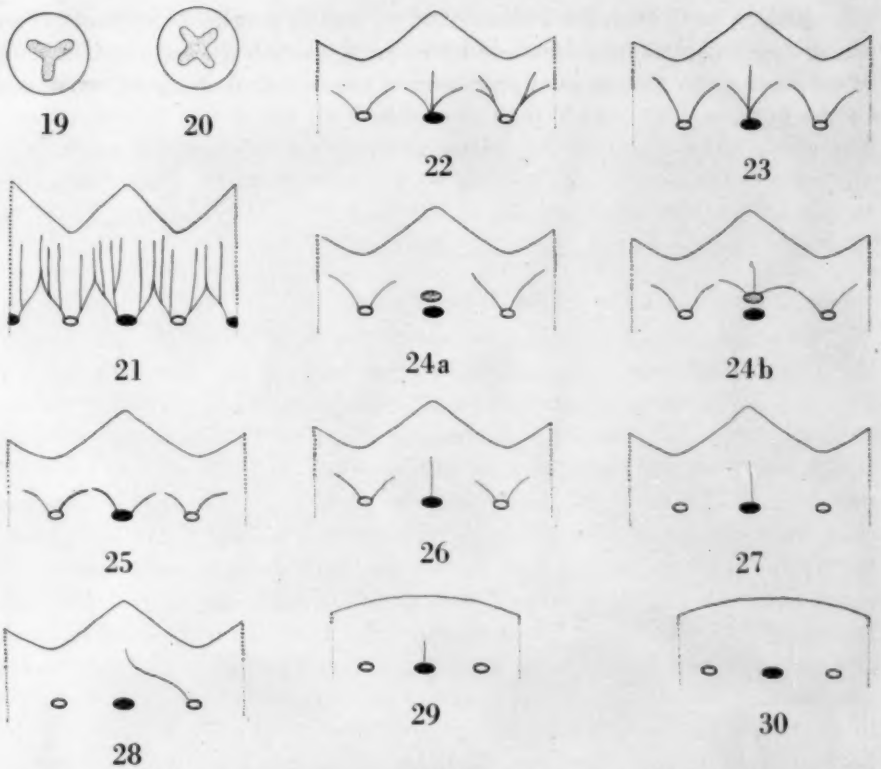
Explanation of figures 8–18

Variations in the ovular supply as seen in X-sections of the ovary. In these diagrams, the arching indicated in fig. 1 is telescoped onto one plane. FIG. 8. *C. florida.* Heavy, scarcely arching ovular traces. FIG. 9. *C. mas.* Heavy, slightly arching ovular traces. FIG. 10. *C. canadensis.* Ventral traces terminate in the ovular traces. (Vestigial ovular traces are drawn here for clarity and convenience); ovular traces heavy. FIG. 11*a–e*. *C. succica. a–e,* stages found in different specimens showing the fusion of the pair of ovular traces supplying separate ovules. *d,* ovule supplied by ovular trace from one side of the carpel only, the corresponding ovular trace not reaching into the septum; one ovular trace gives indication of branching. *e,* as in 11d, but all of the traces enter the septum. FIG. 12. *C. controversa.* Light ovular traces which branch; vestigial ovular traces. FIG. 13. *C. brachypoda, C. rugosa.* Periclinal arc of bundles in the wall of the ovary; branching of the ovular traces; vestigial ovular traces. FIG. 14. *C. racemosa.* Heavy ovular traces; small vestigial ovular traces; narrow arc of bundles. FIG. 15. *C. alsophila.* Heavy ovular traces; vestigial ovular traces; arc of bundles. FIG. 16. *C. stolonifera.* Light ovular traces. FIG. 17. *C. stolonifera.* Branching of ovular traces. FIG. 18. *C. stricta.* Light ovular traces which branch.



FIGS. 19, 20. Types of stylar canals. FIG. 19. 3-lobed stylar canal. FIG. 20. 4-lobed stylar canal. FIGS. 21–30. Types of sepals and sepal supplies. The heavy stippling of the cuts indicates the extent of the calyx; the light stippling, the ovary proper. Outline bundles are petal bundles; solid black bundles are stamen bundles or traces; stippled bundles are sepal traces. In figs. 22–25, the union of the sepal traces derived from the stamen bundles and the adjacent petal bundles is not indicated since it is for so short a distance, and the sepal traces themselves quite short. FIG. 21. *C. florida.* Relatively long calyx tube; sepal traces cut off radio-tangentially from the stamen and petal bundles; sepal traces branching freely and anastomosing in the calyx tube. FIG. 22. *C. Drummondi.* Sepal traces derived from both stamen and petal bundles; both branching. FIG. 23. *C. mas, C. glabrata, C. brachypoda.* Sepal traces derived from the stamen and petal bundles, the trace from the stamen bundle branching. FIG. 24*a*, *b*. *C. stricta. a*, single sepal trace from stamen bundle, two sepal traces from petal bundle. *b*, branching of the sepal trace derived from the stamen bundle. FIG. 25. *C. racemosa.* Two unbranched sepal traces from stamen and petal bundles. FIG. 26. *C. Amomum.* Typical 3-traced sepal—middle trace cut off centrifugally from stamen bundle; two sepal traces cut off radially from petal bundle. FIG. 27. *C. canadensis, C. stolonifera, C. suecica.* Sepal trace only from stamen bundle and this unbranched. FIG. 28. *C. suecica.* Sepal trace from one of petal bundles adjacent to sepal; no sepal trace from the stamen bundle. FIG. 29. *C. controversa, C. stolonifera.* Single sepal trace derived from stamen bundle, but terminating in the ovary wall. FIG. 30. *C. alternifolia, C. suecica, C. stolonifera.* No sepal traces cut off.

(fig. 10). As in *C. mas*, the ovular bundle remains single. At opposite sides of the upper part of each locule in a line parallel with the septum is a band of enlarged cells. Also in the upper part of the ovary, showing no constancy in the bundles with which they are associated, the dorsal traces appear. The single sepal trace, which passes through the microscopic calyx tube and ends in the base of the calyx tooth, is derived from the stamen bundles. In this species, the petal bundles do not give off sepal traces (fig. 27). The petal trace continues unbranched in the petal.

4. C. SUECICA L. *Fernald & Wiegand 5965* (C).

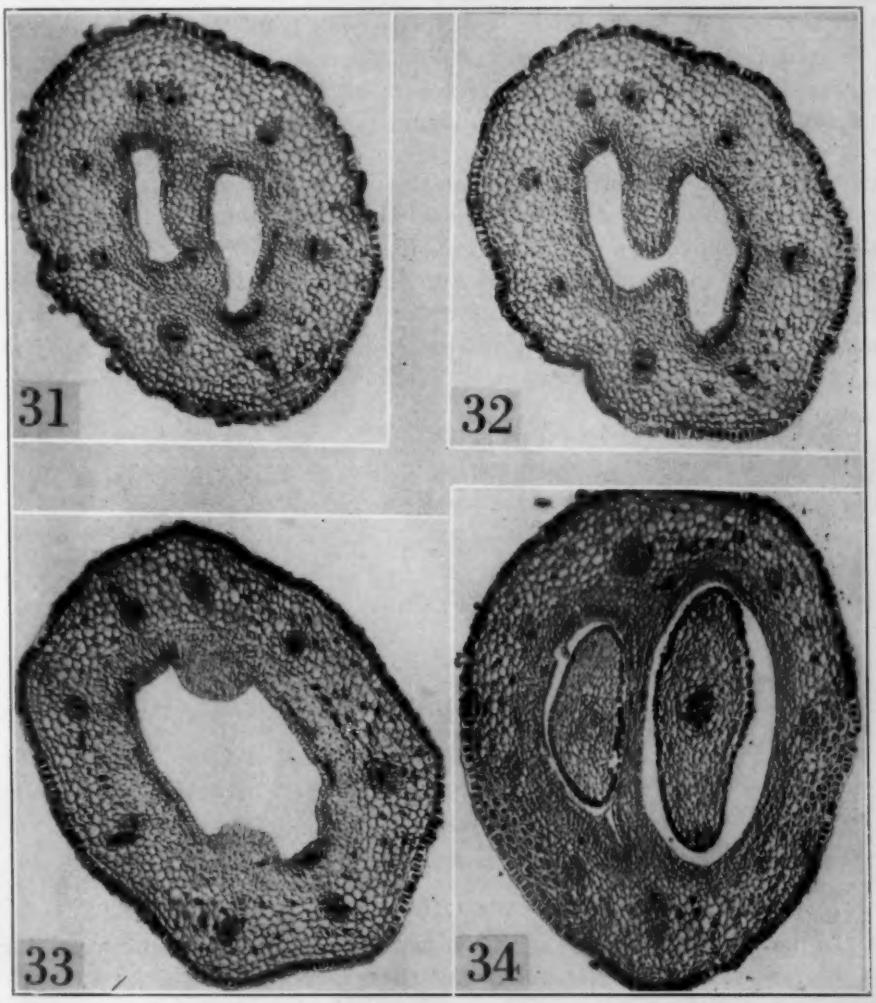
The ventral traces of *C. suecica*, except for their union through most of the length of the ovary, resemble the ventral traces of the preceding species. This species, moreover, displays the most extreme fusion of the ovular traces. In it, the "foreign" ovular traces (those of the two carpels) are fused almost to the center of the septum where they separate in joining their "sister" ovular traces (those of the same carpel) (figs. 11a–11c). In one extreme case, one ovular trace does not reach into the septum (fig. 11d); in another, the ovular trace extending into the septum fails even to turn toward its respective ovule (fig. 11e). As in *C. mas* and *C. canadensis*, the ovular bundle remains single. The dorsal traces usually arise from the petal bundles but a few seem to be derived from the stamen bundles. Though in half the flowers examined, the sepal supply is similar to that of *C. canadensis*, the condition in the other half shows interesting deviations from that of this species. In four flowers some (one, two, or three) petal bundles divide as well as the stamen bundles. Of these flowers, two have stamen bundles which do not divide. In the first such flower this is true of two stamen bundles, and the corresponding sepal either is without vascular tissue (fig. 30) or it derives its single trace from one of the adjacent petal bundles (fig. 28). In the second flower only one stamen bundle remains undivided. Here the supply to the corresponding sepal is again derived from the adjacent petal bundle (fig. 28).

This last flower differs in another respect from the other flowers of this genus. Its ovary lacks a septum. At the base of the ovary is a septum separating the two small locules (fig. 31). Shortly, however, the septum separates into two protuberances extending from the ovary wall into the locule (fig. 32). Each of these projections is covered by an epidermis continuous with that lining the ovary wall. These projections recede toward the ovary wall (fig. 33) and finally disappear so that in the upper half of the ovary there is no evidence of their presence below. There are no ventral bundles and no ovules in this ovary.

In this species, the petal supply does not differ from that of *C. canadensis*.

5. C. CONTROVERSA Hemsl. *Steward & Cheo 231* (NY).

This and the following species are the two alternate-leaved species in the genus. In this species, the ventral traces separate from the two opposite petal



FIGS. 31–33. *C. suecica*. Cross section of the ovary at three successively higher levels showing incomplete septation of the ovary—the septum complete at the base, but receding acropetally toward the ovary wall. In fig. 32, the appearance is that of two parietal placentae. FIG. 34. *C. suecica*. Cross section of ovary showing abortive carpel and ovule.

or stamen bundles, and behave as described in the generalized floral type. Both these species differ from the opposite-leaved species studied in the shape of the septum in the upper part of the ovary. Whereas in transverse

section the septum of other species is usually a band of tissue separating the two locules, in this pair of species, the septum is swollen, each side protruding into its respective locule (fig. 38). Consequently, the locule appears as a narrow crescent. In the lower part of the ovary, the dorsal traces, together with numerous lateral traces, separate from the peripheral ring of bundles. Since these unite in varying degrees at the top of the ovary, it is difficult to decide how much of the dorsal strand in the style consists of the distal portions of one or more lateral traces. The calyx consists of a mere rim or short tube, which is scarcely perceptible macroscopically. Moreover, the rim or tube is devoid of vascular tissue; for though in all the flowers examined some of the stamen bundles divide, all of the centrifugal traces so formed terminate in the ovary wall (fig. 29). In only one flower do all four stamen bundles divide; two flowers have three dividing. A flower with two and one with a single stamen bundle branching were also found. The non-dividing stamen bundles are as large as the dividing ones before the latter fork. None of the petal traces divides.

6. C. ALTERNIFOLIA L.f. *A. J. Eames 2957* (C).

Since this species differs anatomically from the preceding one only in having certain characters more reduced, it will suffice to list these:

1. The ventral traces are fused and break up into fewer traces at the region of ovule attachment.
2. The ovular bundle remains unbranched in the ovule.
3. There are fewer lateral traces.
4. The dorsal traces separate from the peripheral bundles in the upper part of the ovary.
5. The stamen bundles do not divide (fig. 30). Though this is generally true, a few flowers show one or two stamen bundles dividing. For the most part, therefore, there is neither external nor internal manifestation of the calyx. Nevertheless, as in *C. controversa*, the stamen bundles are manifestly stouter than the petal traces.

7. C. OBLONGA Wall. *A. Henry 11,161* (NY).

In the single bicarpellate specimen examined, the petal bundles give rise to the ventral traces. These differ from those of the generalized floral type in ending as mere stubs in the upper part of the ovary. The ovular supply also differs, for the ovular trace descends below the funiculus and then arches upward in entering the ovule. Poor differentiation makes it difficult to discern the association of the dorsal traces. The sepals apparently derive their supply from both stamen and petal bundles.

The other two serials were buds of tricarpellary flowers (fig. 35). In one, two ventral bundles separate above the base of the locule and are fused as

far as the top of the ovary but the third originates double at the base of the ovary; in the other bud, the three ventral bundles are similar; each is composed of the ventral trace of one carpel and the adjacent ventral trace of the carpel beside it, and each arises at the base of the locule. The ovular bundle

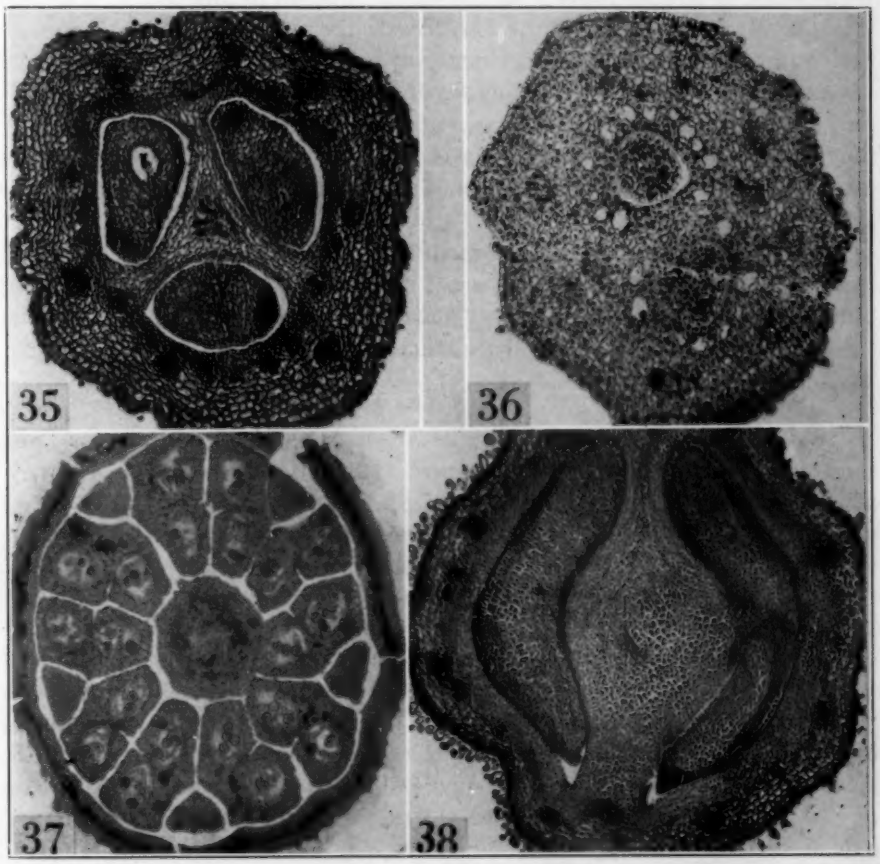


FIG. 35. *C. oblonga*. Cross section of a tricarpellary ovary. FIG. 36. *C. mas*. Large secretory cells surrounding the locules. FIG. 37. *C. Drummondi*. 5-merous flower showing 5 petals and 5 stamens. FIG. 38. *C. controversa*. Septum swollen at region of ovule attachment.

is single. Poor differentiation again makes it almost impossible to determine with which bundles the dorsal and ventral traces are associated. The exact sepal situation is also obscure. Several of the stamen bundles resemble those of *C. mas* in their behavior. The petal trace forms about three strands after entering the petal.

8. C. DRUMMONDI Meyer. *C. C. Deam 48559* (C) (as *C. asperifolia*).

The ventral traces of this species, though extremely variable, seem to come principally from the stamen bundles and tend to be separate most of their length. Regularly, however, they enter the style. Though the dorsal trace seems to be associated with the stamen bundle in one flower, in others it is difficult to trace. Among the *Thelycrania* the sepal supply of this species, besides being variable, is the most extensive and complex (fig. 22); the sepal traces derived from the petal bundle often branch and the stamen bundle may divide radially as well as tangentially. The trace cut off tangentially may cleave into three branches as in *C. mas* (fig. 23), or it may give off just a single lateral branch. Various combinations and intergradations of these types of supply are encountered.

One flower of this species is 5-merous (fig. 37). Since it has a bicarpellate ovary, its carpellary supply is not unusual. The number of peripheral bundles in the body of the ovary, however, is ten instead of eight. Anatomically, therefore, it differs little from the general pattern in the genus.

9. C. BRACHYPODA Meyer. *C. Y. Chaio 2632* (NY) (as *C. macrophylla*).

In this species, the ventral bundle arises at the base of the ovary and the traces remain fused the greater part of their length. The supply thereafter is that described for the generalized floral type (fig. 13). The dorsal traces separate from the two stamen bundles alternating with those from which the ventral traces arise. The sepal supply of this species resembles that of *C. mas* (fig. 23).

10. C. GLABRATA Benth. *A. Kellogg 1866* (C).

The ventral bundles are quite variable in this species. In one flower, both ventral bundles arise at the base of the ovule; in two flowers, one ventral bundle separates in the lower part of the ovary, the other in the upper. All, however, are associated with stamen bundles and remain united to the top of the locule. Except that the ovular traces are only slightly bowed and scarcely arched, the ventral and ovular supply differs little thereafter from that of the generalized type. The absence of lateral traces aids in following the dorsal traces to their origin from the stamen bundles. The sepal supply is rather consistently like that of *C. mas* (fig. 23). All but one stamen bundle divide tangentially; the exceptional stamen bundle has a trace separating radially from each side.

11. C. RACEMOSA Lam. *J. H. Kellogg 423* (C) (as *C. paniculata*).

The ventral traces separate at the base of the ovary from the stamen or petal bundles. The arc of ovule traces is not so wide as that of the generalized floral type nor do the ventrals enter the style (fig. 14). In the ovule, the

ovular bundle forks before dividing further. Since there are numerous lateral traces in this species, it is difficult to distinguish the dorsal traces from these. The sepal supply seems to be derived from one like *C. mas*. Instead of dividing tangentially to give a trace which gives rise to a lateral branch on each side, however, one or two stamen bundles in each flower cut off a trace from both ends (fig. 25). The plane of division may be tangential or almost radial.

12. C. STRICTA Lam. *W. S. Blatchley 39* (C).

The ventral bundles of this species are even more variable than those of *C. glabrata*. They may separate in the lower or upper part of the ovary, from the stamen or petal bundles, or both; they may be fused up to the departure of the ovular traces—or one ventral bundle may be double, the other, united; finally, they may end in the ovary or enter the stylar column. The dorsal traces also arise either from petal or stamen bundles. There are no lateral traces in the carpels. Though the vascular supply to the sepal is very similar to that of *C. mas*, it differs in that a single bundle is derived tangentially from the stamen bundle (fig. 24a). This bundle then gives off a lateral branch on each side (fig. 24b). These side branches, like those of *C. mas*, unite with the adjacent trace from the nearby petal bundle.

13. C. ALSOPHILA W. W. Smith. *J. F. Rock 17,228, 16,142* (NY).

It is the stamen bundles, in this species, which are united at the base with the ventral traces. The latter are sometimes fused, sometimes separate. Except that the ovular bundle branches sparingly, the behavior of the ventral supply is very similar to that in the generalized flower type (fig. 15). The rest of the carpellary supply consists of dorsals, which are difficult to follow to their origin. The sepal supply is sometimes like that of *C. mas* (fig. 23), sometimes simply three-traced.

14. C. RUGOSA Lam. Flora of Northern U. S. *376* (C) (as *C. circinata*).

From their origin from the stamen bundles, the ventral traces remain separate and thereafter resemble the ventral traces of the generalized type in their behavior (fig. 13). The dorsal traces are associated either with the stamen or petal bundles, and like the laterals, are weakly differentiated. Unlike the sepal supply in most species described, the derivation of sepal traces from the petal bundles is quite similar to that of the stamen bundles, for usually each stamen and petal bundle gives rise to two sepal traces.

15. C. AMOMUM Mill.

The ventral traces of this species resemble those of *C. glabrata* in their variability. Though they regularly arise from the petal bundles, they vary in the extent of union of the two unrelated ventral traces, for fusion of the traces both half the length of the ovary and the full length are encountered.

Moreover, in two flowers both conditions appear in the same ovary. The ovular traces are extremely heavy, and are bowed and arched only slightly as compared with the ovular traces in the generalized floral type. Within the ovule, the ovular bundle forks, then branches distally. For the most part, the intermediate strands of the ventral bundle are not distinct strands, for they join with the ovular traces and with one another. Because the cells of the ovary are abundantly supplied with mucilage, and since the mucilage stains with crystal violet as does the vascular tissue, the origin of the dorsal traces is obscured. However, in part of the serials examined, the dorsal traces seems to be connected with the petal bundles. Difficult to distinguish from the dorsal traces are a few lateral traces. The sepal trace is evidently derived from a three-traced type, i.e., one having a trace from the stamen and each of the two adjacent petal bundles. Yet it is evident from the diversity seen that the sepal supply is not yet stabilized; for though only one or two sepals in each flower are truly three-traced (fig. 26), there are various intergradations between a completely 3-traced sepal and a sepal with a single trace from a stamen bundle. One flower has one sepal 3-traced and the rest simulating a 3-traced supply with a branched trace from the stamen bundle similar to that of *C. mas*.

16. C. STOLONIFERA Michx.

In this species, the ventral traces usually separate at the base of the locule from the stamen bundles and continue fused for the greater part of their length. They may, however, separate at the base of the receptacle; they may be derived from petal bundles; and the ventral traces may be united and separate in the same ovary. There are few intermediate ventral strands at the level of the funiculus and the ovular traces are rather light (fig. 16). The ramification of the ovular bundle is the most extensive encountered (fig. 4). Rather peculiarly, the phloem of the ovular trace is on the adaxial surface of the carpel rather than the abaxial side, as might be expected. The dorsal traces diverge from the stamen or petal bundles. There are no lateral traces. Next to *C. alternifolia*, the sepal supply is most reduced in this species. With the exception of a petal bundle which gives off a single trace radially, the petal bundles do not divide. With respect to the sepal traces from the stamen bundles, only two or three stamen bundles divide (figs. 27, 29, 30). These cut off a single trace which may enter the sepal or terminate in the ovary (figs. 27, 29). One stamen bundle was found which split into three branches. Within the petal, the petal bundle divides into several strands.

DISCUSSION

The marked variation in the floral anatomy of the species described contrasts strikingly with the strong similarity in their gross floral morphology. This variation is seen in the bundles from which the ventral and dorsal

traces separate, in the number of lateral traces present, and in the vascular supply of ovules, petals, and sepals.

Petal Supply. That the vascularization of the petal is undoubtedly secondary is evidenced by two characteristics of such a petal supply. Regardless of how extensively the petal bundle branches, there is always just a single petal trace, which divides only after entering the petal (fig. 6). This vascularization seems to be coincident with the reduction of the calyx and the enclosure of the androecium and gynoecium by the corolla.[2] This is not to say, however, that the reduction of the calyx caused the ramification of the bundle in the petal.

Most of the other variations, however, are of such a nature that, together with other features of the floral anatomy, they point to a derivation of the genus from a group of plants whose floral structure was quite different from that of *Cornus*. Moreover, there is evidence not only for the structure of the ancestors of this genus, but also for the direction of development in the structure of its descendants: or more simply, there is evidence of evolution progressing as well as past.

Ancestral Flower. There is evidence to believe that the ancestral flower had more members in each whorl than the flower of the present genus. The 5-merous flower found in *C. Drummondi* (fig. 37), and the 3-carpellate ovary in two specimens of *C. oblonga* (fig. 35) and a flower of *C. mas* can be cited. The theory is further supported by the gross floral structure of other genera of the family, for *Mastixia, Toricellia, Helwingia, Corokia, Griselinia,* and *Melanophylla* have 5-merous flowers; and 3-carpellate flowers are found in *Toricellia, Helwingia,* and sometimes *Melanophylla.* These facts would suggest therefore that the ancestral flower was 5-merous.

Interesting light is cast on this point by the variation in the bundles with which the ventral bundles are united. These may be derived from the stamen bundles, as is always the case in *C. canadensis, C. rugosa, C. glabrata, C. brachypoda,* and *C. suecica;* they may be associated with the stamen bundles in some flowers and the petal bundles in other flowers of the same species, as in *C. alternifolia, C. florida,* and *C. stolonifera,* or in the same flower one may separate from the petal bundle, the other from the stamen bundle, as in some specimens of *C. Drummondi, C. controversa,* and *C. mas.* The dorsals likewise, both among the various species and among the various flowers of the same species, vary in the bundles with which they are fused. This wide variation is indeed unaccountable in a flower as regular as that of this genus. On the other hand, if one assumes that the flower of *Cornus* has been derived from a 5-merous flower, the extraordinary variation becomes explicable. In

[2] A similar condition of reduced sepals and highly vacularized petals is found in *Hedera Helix* and species of *Alangium.*

a reduction from five to two carpels, either two adjacent carpels, or a carpel and either alternate carpel would persist. Such a reduction would result in an ontogenetic rearrangement of the carpels. The developing carpels would vary therefore in their orientation with respect to the outer whorls. Coupled with this decrease in the number of carpels would be the reduction of the outer whorls from five to four members. These two changes interacting with each other would make the various combinations described above quite possible; and the ontogenetic nature of these changes might explain the instability within a species and among them.

Vestigial bundles are often the only remnants of structures once present. In *C. alsophila, C. brachypoda, C. florida,* and occasionally in other species, one or two traces terminate in the receptacle; yet since there is so little uniformity in their position, number, and grouping, it is difficult to discover their essential character. This lack of uniformity may, as above, be due to the reduction in the number of the members of the floral cycles. Nevertheless, whatever their exact nature, they are an indication of other members of the floral whorls now absent.

On the other hand, the abortive carpel found in specimens of *C. florida* and *C. canadensis,* and all the specimens examined of *C. suecica* (fig. 34), suggest that this reduction is proceeding in the present-day members of the genus. Again, this change is to be seen already in other members of the family (*Mastixia, Aucuba, Griselinia*).

Calyx in the Ancestral Flower. The sepal supply suggests that the calyx also has had an interesting evolution. In the genus today, the calyx is usually small; it consists of four teeth or lobes in most species and of a mere rim in a few. Anatomically, however, in most of the species, especially the three-traced ones, the sepal supply is extraordinarily extensive and heavy for sepals so minute.

C. florida is conspicuous in the extreme vascularization of its calyx. Here both the traces derived from the petal bundles and those from the stamen bundles branch freely, providing many bundles in the calyx (fig. 21). So extensive a supply is approached only by *C. Drummondi* (fig. 22). In *C. mas,* (fig. 23), on the other hand, only the trace cut off by the stamen bundle divides. In this respect, several other species resemble it, viz., *C. brachypoda, C. glabrata, C. racemosa, C. stricta* (fig. 24b), *C. alsophila,* and *C. oblonga.* In *C. Amomum* (fig. 26) there is no ramification of the three traces, and intermediate between this condition and that in *C. mas* is the supply of *C. rugosa.* The reduction has proceeded in *C. canadensis* (fig. 27) and some specimens of *C. suecica* (fig. 27) to an elimination of the two lateral traces, so that the sepal is supplied only by a median trace derived from the stamen bundle. In the two alternate-leaved species and in *C. stolonifera,* some of the stamen bundles even fail to divide (fig. 30). Moreover, in bundles that

do divide, the trace which in other species enters the sepal, here terminates in the ovary (fig. 29).

It is evident, therefore, that in these species of *Cornus* there are sepals with a single trace and sepals with three traces.[3] However, this distinction cannot be used to divide the genus, since specimens of *C. stolonifera* and *C. suecica* (fig. 28) occasionally show traces derived from petal bundles. Moreover, such a division would result in a grouping of *C. suecica, C. canadensis, C. controversa, C. alternifolia,* and *C. stolonifera;* an exceedingly unnatural grouping, for it separates *C. stolonifera* from the rest of the *Thelycrania* and places the two alternate-leaved species in the same division as the two suffrutescent species. Nevertheless, the one- and three-traced conditions together with their variations are significant, for they indicate the trend in the reduction of the sepals.

Anatomy suggests that the sepals of the ancestral flowers were foliaceous. Externally they have become very small, and, correspondingly, the vascular supply has become less extensive. But in many species, this internal reduction has not proceeded so far as the external one. In addition, the extreme reductions observed indicate that this reduction will tend toward a disappearance, not only of the sepals themselves, but also of the sepal traces.

Nature of the Septum. Superficially, this genus has a bilocular ovary with axile placentation; actually, observations almost necessitate the conclusion that the ovary was once unilocular with two well-developed parietal placentae.

Most of the species today show no special histological development of the placenta: the placenta is apparently only a locus. In the two alternate-leaved species, however, the swelling of the septum at the region of ovular attachment can only be considered as placental in nature (fig. 38). But this placenta is not a typically axile one.

Even the anatomy is that of parietal rather than axile placentation. In all the species studied, the ventral traces never turn inward in the receptacle, as is the case in axile placentation. Instead, from the receptacle, they proceed directly toward the ovary wall (fig. 1). Moreover, the ventral traces remain in the ovary wall, in no case entering the septum (figs. 3, 4).

In itself, the specimen of *C. suecica* with incomplete septation of the ovary is insufficient evidence for parietal placentation; in view of the above facts, however, the specimen is quite suggestive. Here, the two projections into the locule have the position of parietal placentae (fig. 32). They do not extend to the top of the ovary, a fact which may account for the absence

[3] The interpretation of the type of sepal supply found in *C. rugosa* as 3-traced is supported by the fact that the leaves of the members of this family are regularly 3-traced (12), and that 3-traced sepals are found in species less advanced in other characters also. It is worthy of note that the reduction to the single trace has taken place in the sepals before it has occurred in the vegetative member.

of ovules and non-separation of the ventral traces from the outer ring of bundles.

Anatomy also indicates that the placenta was once more extensive than it is today. Significant in this respect is the number of traces derived from the ventral bundle at the region of ovule attachment. In some species, there are many branches, but only a few actually enter the ovules. The other branches are undoubtedly also ovular traces, for they are identical with the traces supplying the ovules, in derivation, position in the ovary, and course—they differ, in fact, only in not entering an ovule (fig. 1). Moreover, occasional flowers of *C. alternifolia*, *C. suecica* (fig. 11d), *C. stricta* (fig. 18), and *C. stolonifera* (fig. 17) show a branching of an ovular trace. This indicates that at one time these were placental bundles which probably branched. Finally, the periclinal arc of ovular traces found at the level of ovule attachment in the ovary wall of some species [*C. controversa*, *C. alternifolia*, *C. brachypoda* (fig. 13), *C. racemosa* (fig. 14), *C. rugosa* (fig. 13), *C. glabrata*, *C. stricta*, *C. Drummondi*] indicates that the placenta might have covered more of the ovary wall than it does at present. Besides extending periclinally, the placentae must also have reached well into the locule for fusion to have occurred.

The septum, therefore, is placenta rather than ovary wall: It has resulted from fusion of two parietal placentae rather than fusion of parts of the walls of the two carpels.

Ovule—Evolutionary Changes. From the vestigial ovular traces, it is clear that the uniovulate carpel of *Cornus* is descended from a multiovulate carpel. Anatomy indicates, in most species, that it is an outer ovule which persists. First, in the species studied, the vestigial ovular traces, when present, are included between the functional ovular traces (figs. 13, 14). Secondly, some species show a bowing of the ovular traces (fig. 13). This bowing may mean that the ovule has moved toward the center, since ordinarily, an ovule so situated with respect to the ventral trace would have a trace running directly to it.

The reduction in the number of ovules has complicated the supply of the surviving ovules, for unlike most ovules, the ovule of *Cornus* receives a bilateral supply, i.e., it receives a trace from each of the two ventral traces of the carpel. In some species, these two bundles are distinct within the ovule. This double supply can only mean that, recently in the phylogeny of the group, each carpel had two ovules, one on each margin. When one of the ovules no longer develops, its persistent ovular trace enters the remaining ovule. In several species some of the intermediate traces fuse with the outer traces, which supply the ovules. In these species, the ovule receives the supply of not two, but several ovules. The extraordinarily heavy bundles in many of the species [*C. florida* (fig. 8), *C. canadensis* (fig. 10), *C. alsophila*, *C.*

glabrata, C. Drummondi, C. racemosa (fig. 14), *C. stricta*] represent without doubt advanced stages of fusion of the intermediate and outer ovular bundles.

There is also evidence for the direction in which the ovary may evolve. The occasional flowers with an abortive ovule (*C. canadensis, C. Drummondi, C. suecica* (fig. 34)) forecast a uniovulate ovary. Accompanying this reduction in gross structure will probably be a reduction in the vascular supply. *C. suecica* can be cited as evidence for this, for here are found fusion of the ovular traces derived from the same ventral bundle (figs. 11a–11e) and occasionally elimination of the double supply to the ovule (fig. 11d).

Conclusions of Other Students of the Family. As stated in the introduction, the little that has been published in the floral anatomy of the *Cornaceae* has come from Horne, Martel, and Baillon. Of these, Horne and Martel have dealt with *Cornus*.

Horne (8) has made a comparative study of ten genera of the *Cornaceae*. Several of his observations and conclusions are of interest in connection with the observations and conclusions recorded above. He considers the possibility that the style may be composed of the styles of four carpels and gives Clarke's interpretation of the 4-lobed stylar canal. Clarke (4) concluded from his observations that the styles of two carpels made up the style. In the 4-lobed stylar canal, he interpreted two of the canal lobes as "marginal" and two "sutural." Moreover, Clarke found that in a trilocular ovary there were two additional lobes in the stylar canal for each extra locule, one "marginal," one "sutural."

In the present study, though no special study of the style was made, the shape of the stylar canal was recorded for each specimen. In many species, the stylar canal varies in shape from base to apex. Just above the locules, the canal in transverse section is more or less linear, gradually becoming S-shaped, Y-shaped, and H-shaped in turn, and at the very apex, 4-lobed (fig. 20). In *C. alsophila, C. Amomum, C. Drummondi, C. controversa, C. glabrata, C. brachypoda,* and *C. stricta,* the canal is eventually H-shaped or 4-lobed. However, in *C. alternifolia, C. canadensis, C. florida, C. mas,* and *C. suecica,* the stylar canal remains more or less linear throughout the style. Contrary to Clarke's observations, all the 3-loculate ovaries found have 3-lobed stylar canals (fig. 19). An explanation therefore is required which will account for 3-lobed stylar canals in tricarpellary ovaries of this genus, and 4- or 2-lobed (linear) stylar canals in bicarpellary ovaries. Clarke's interpretation does not adequately explain these observations. Rather than that two stylar canal lobes are associated with a style, it seems more likely that one canal lobe corresponds to each style. Where three carpels are present, there is a 3-lobed stylar canal; where two carpels, a 2-lobed (linear) stylar canal. Where four or more stylar canal lobes are found, the situation is more complicated. It is quite evident that the flower of *Cornus* has been

derived from a polymerous flower, which in many cases has been a completely tetramerous one. Vestiges of the polycarpellary or 4-carpellary condition may therefore be expected. Now, it is common for cohesion to occur acropetally, so that a compound pistil may have several separate styles; a corolla tube, several lobes distally. May not reduction, therefore, proceed in the same direction? The basal part of a carpel may be submerged and disappear before the styles. This would explain the presence of a 4-lobed stylar canal in a bicarpellary pistil: two of the styles are sole remnants of their respective carpels. More light might be thrown on this problem by a special study of the vascular supply of the style in the various species. The problem is complicated, however, by the presence of ventral traces in the base of the style and the secondary ramification of the dorsals in the upper part of the style.

With respect to the other genera that Horne studied, several interesting correlations present themselves in placentation and ovular supply. Evidence for parietal placentation can be found. First, in *Aucuba,* when an ovary is biovulate the two ovules are attached on opposite sides of the ovary wall, so that the placentation is parietal. Also, a situation parallel to the abnormal ovary of *C. suecica* is found in some specimens of *Marlea.* In this genus Bentham and Hooker (2) state that the ovary may be unilocular in the upper and trilocular in the lower portion. Clarke also noted this condition, in *M. begonifolia.* Finally, Horne lists as a difference between *Cornus* and *Corokia* the fact that the latter genus has parietal placentae immediately above the ovule. In view of the discussion above, this would be considered a similarity! On the other hand, two pieces of evidence may be cited in favor of axile placentation. First there is the very definite axile placentation in *Helwingia.* Neither Horne nor Descaisne (5), however, believes that this genus belongs in the *Cornaceae.* A more cogent objection is the central strand in the septum of *Corokia.* Since the origin of this strand is not given in Horne's paper, however, material must be examined before an explanation is ventured.

The compound ovular supply of *Cornus* is seen in *Corokia, Griselinia, Nyssa* also, and to a limited extent in *Aucuba.* Horne also recognizes that (in *Corokia*) there may be a "diversion of the vascular tissue pertaining to the absent ovules to the present ovule."

Whereas Horne has studied a majority of the genera of the *Cornaceae* Martel (11) has studied a single species of *Cornus,* upon which he bases his comparison of the family with the *Araliaceae* and the *Umbelliflorae.* Moreover, Martel emphasizes histological structure and is thereby led to erroneous or superficial statements. For example, he states that except for the vascular supply, the calyx, with respect to the parenchyma of which it is made up, can be considered simply a prolongation of the receptacle. (As will be seen, Martel believes the ovary is enveloped by the receptacle.)

He considers that the 4-lobed stylar canal indicates that there are four carpels, but states that they are reduced at the base by atrophy or fusion following upon a limitation in the space allowed them to develop. He does not make clear whether he believes this atrophy or fusion to be ontogenetic, or phylogenetic.

He concludes that the placentation is parietal, because the "placental" bundles remain in the ovary wall. Like Horne, he does not recognize these "placental" bundles ("peripheral" bundles of Horne) as the ventral bundles. In fact, he even states that the "commissural" (ventral) bundle is absent.

With respect to the bilateral ovular supply, he states that it is notable that the "funiculi" (ovular traces) derived from both placentae of the carpel enter the same ovule, just as if the placentation were axile. It is assumed that he means that type of axile placentation in which the two ventral traces of a carpel have fused. Yet what evidence is there to believe that in such cases the ovular supply is bilateral, i.e., composed of an ovular trace from each of the two ventral traces of the carpel? In fact, there is evidence to the contrary. First, in axile placentation, the ventral traces of adjacent carpels unite more commonly than do the ventral traces of the same carpel. Moreover, even when the ventral traces of the same carpel are separate, it is very unusual for an ovule to receive a trace from each ventral trace. There is little basis, therefore, to conclude that after the ventral traces have united, the ovular trace is double. Martel's parallelism is, therefore, merely an analogy and can have little significance in establishing the type of placentation found in *Cornus*.

Martel interprets the separation of the outer ring of bundles from the carpellary bundles as a more marked separation of receptacle and ovary in *Cornus* than is found in the *Umbelliflorae*, *Hedera*, and *Aralia*. Had Martel examined other species of *Cornus* and observed how often the dorsal traces are united with the peripheral bundles the length of the ovule, he would have avoided such a generalization. He states, furthermore, that from the inferior ovary of *Cornus* to a superior ovary it is only a short step, which consists simply of a more profound differentiation of perianth and androecium. Such a differentiation could only be from the outer portion which he considers receptacular. Stamens, petals and sepals so formed would be appendicular in nature in the upper portion and axial in the lower portion. These would indeed be anomalous floral members.

Taxonomy. A comparative study of the floral anatomy of a group should reveal the extent of specialization of the various members so far as their flowers are concerned, thus aiding in establishing the relationship among them. It must be remembered, however, that all the characters of a species do not evolve at the same rate; in fact, some may, for a time, remain

unchanged or even retrogress. Moreover, changes vary in their significance, both in themselves, and in comparisons among different species. For instance, in the species of *Cornus*, the supply of the petal is of little phylogenetic importance, as compared with the variation in the supply of the ovule. On the other hand, though the extent of fusion of the ventral traces is in itself significant in indicating evolutionary advancement, it can scarcely be used in this genus, since the character often varies within the species itself. The situation in the sepal supply is quite the reverse, for here the degree of change, important in itself, is consistent within the species. In evaluating the relative progress of the various species, therefore, the sum total of the various advanced traits together with their significance must be considered.

Among the species studied, *C. florida* is anatomically by far the least specialized. It has the most extensive sepal supply (fig. 21); the ovule supply is very heavy (fig. 8); and without exception there is a "vestigial" trace in the receptacle. In other species such traces occur only occasionally, if at all. At the other extreme are the anatomically highly specialized *C. alternifolia* (fig. 30), *C. stolonifera* (fig. 30), and *C. suecica* (fig. 30). In all three, the vascular supply to the calyx is absent or incomplete. *C. alternifolia*, with no sepal traces and the calyx reduced to a mere rim, shows the most extreme reduction externally as well as internally. In ovule supply, all three have relatively light ovular traces, but *C. suecica* shows the most specialized condition (figs. 11a–11e). Moreover, *C. suecica* regularly shows the abortion of one ovule and often a decrease in size of the corresponding carpel (fig. 34). Of the three, therefore, this is probably the most highly specialized.

In Wangerin's treatment (13), the species studied fall into the following sub-groups:

Subgenus *Benthamidia*
- *C. florida*

Subgenus *Macrocarpium*
- *C. mas*

Subgenus *Arctocrania*
- *C. canadensis*
- *C. suecica*

Subgenus *Thelycrania*
- Section *Bothrocaryum*
  - *C. controversa*
  - *C. alternifolia*
- Section *Amblycaryum*
  - Subsection *Albidae*
    - *C. racemosa*
    - *C. stolonifera*
    - *C. Drummondi*
    - *C. rugosa*
    - *C. glabrata*
    - *C. stricta*
  - Subsection *Oblongifoliae*
    - *C. oblonga*
  - Subsection *Nigrae*
    - *C. alsophila*
    - *C. brachypoda*
  - Subsection *Corynostylae*
    - *C. Amomum*

The floral anatomy does not strongly support the taxonomic groupings within the genus. The following comparison is based primarily on the sepal supply, since the stages in its evolution are rather completely represented in the species studied. *C. florida* is anatomically sufficiently distinct to be segregated from the other species and in this respect sufficiently unspecialized to represent a type ancestral to them. From this species, *C. mas* may represent a step in the reduction. In this involucrate series, extreme reduction is reached in *C. canadensis* and *C. suecica*. These two suffrutescent species are macroscopically strikingly similar. Microscopically also, in their sepal and petal supply, and in the frequent abortion of one ovule, they are similar. Yet the ovule supply of *C. canadensis* (fig. 10) is so heavy and "primitive" in comparison to the extremely fused supply of *C. suecica* (figs. 11a–11e), that, phylogenetically, the two species must be quite distant. Either they have developed along divergent lines from a "common ancestor," or more likely *C. suecica* has evolved so much more rapidly than *C. canadensis*, that there is now a wide breach between them.

In the non-involucrate species (subgenus *Thelycrania*), the opposite-leaved species are placed in the section *Amblycaryum* apart from the alternate-leaved species. Most of the opposite-leaved species have a sepal supply so similar to that of *C. mas* (fig. 23) or so evidently a modification of such a supply, that it seems quite possible that they have had a common origin close to that of *C. mas*, and a development rather parallel. Anatomically, the members of the section do not segregate into groups. *C. oblonga* has been inadequately studied, but the double arching of the ovular trace makes it unique. Among the rest, *C. Drummondi* (fig. 32) has a sepal supply which, in its extensive ramification, approaches the supply of *C. florida* (fig. 21). The other species more closely resemble *C. mas* (fig. 23). Very similar to the sepal supply of *C. mas* is that of *C. brachypoda, C. glabrata, C. racemosa, C. stricta*. The supply of *C. brachypoda* is most regularly like that of *C. mas*, whereas occasional stamen bundles of the other species diverge from this. Progressive reduction is seen in *C. alsophila, C. rugosa, C. Amomum*, and *C. stolonifera*, flowers of the last species showing some sepal traces absent (fig. 30). In a general way the ovular supply supports the two groupings but there is not enough variation in this character among the species to indicate relative progress among them. The above does not imply that the two groups are considered "natural" or that the members of the section can be arranged in ascending order with *C. Drummondi* at the foot. Rather, these species seem to form a plexus, some of them more advanced than others, but most of them so closely related, phylogenetically, as to make it difficult to select the main lines of development.

The alternate-leaved species are sharply set apart from opposite-leaved species. The internal structure supports this separation, for *C. controversa*

and *C. alternifolia* are characterized by the presence of a prominent placenta (fig. 38), extreme arching of the ovular traces, and short (or absent) sepal traces (figs. 29, 30), which never enter the minute calyx tube or rim. In addition to the above characters, the two species resemble each other in having numerous lateral traces in the carpel. Of the two, *C. alternifolia* is more advanced since it rarely has sepal traces; the calyx is a mere ridge; and the ovular supply is not extensive. The anatomy of the two species is so specialized, however, that it is difficult to be certain anatomically, that the pair are distal twigs on a side shoot of the *Thelycrania* limb of the phylogenetic tree of *Cornus*.

SUMMARY

A detailed study was made of the floral anatomy of sixteen species of the genus *Cornus*.

The evidence obtained suggests the following conclusions:

1. The ancestral flower had more members in each whorl than the flower of the present genus.
2. The sepals in the ancestral flower were foliaceous, in contrast to the minute sepals characteristic of the genus today.
3. The bilocular ovary with reduced placenta is derived from a unilocular ovary with two well-developed parietal placentae.
4. Morphologically, the septum represents two placentae fused.
5. The uniovulate carpel is derived from a multiovulate carpel.
6. The vascularization of the petal is undoubtedly secondary.

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Literature Cited

1. **Baillon, H.** Natural History of Plants, **8**: 66–83. 1881.
2. **Bentham, G. & Hooker, J. D.** Genera Plantarum **1**: 949. 1867.
3. **Chamberlain, C. J.** Methods in Plant Histology ed. 5. 1933.
4. **Clarke, Benjamin.** On the structure of the ovary of *Marlea* and affinities of Alangieae. Jour. Bot. & Kew Misc. **2**: 129–132. 1850.
5. **Decaisne, M. J.** Remarques sur les affinités du genre *Helwingia*, et établissement de la famille des Helwingiacées. Ann. Sci. Nat. II. **6**: 65–74. 1836.
6. **Douglas, G. E.** The inferior ovary. Bot. Rev. **10**: 125–186. 1944.
7. **Eames, A. J.** The vascular anatomy of the flower with refutation of the theory of carpel polymorphism. Am. Jour. Bot. **18**: 147–188. 1931.

8. **Horne, A. S.** A contribution to the study of the evolution of the flower, with special reference to the Hamamelidaceae, Caprifoliaceae and Cornaceae. Trans. Linn. Soc. II. **8**: 239–309. 1914.
9. **Jackson, G.** Crystal violet and erythrosin in plant anatomy. Stain Tech. **1**: 33–34. 1926.
10. **MacDaniels, L. H.** The morphology of the apple and other pome fruits. Mem. N. Y. Exp. Sta. 230: 1–32. 1940.
11. **Martel, E.** Contribuzione all'anatomia del fiore dell' "*Hedera Helix*," dell' "*Aralia Sieboldii*" e del "*Cornus sanguinea.*" Mem. Accad. Sci. Torino II. **58**: 561–579. 1908.
12. **Sinnot, E. W.** Investigations on the phylogeny of the angiosperms. Am. Jour. Bot. **1**: 303–322. 1914.
13. **Wangerin, W.** Cornaceae. *In* Engler, A. Das Pflanzenreich **IV (229)**: 1–110. 1910.

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STRUCTURE AND DEVELOPMENT OF SCLEREIDS IN THE PETIOLE OF CAMELLIA JAPONICA L.

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INTRODUCTION

This paper describes the results of a study of the structure and development of the remarkable thick-walled and grotesquely branched cells which occur in the parenchyma of the leaf of *Camellia japonica*. These elements were discovered and illustrated nearly a century ago by Mirbel and Payen (1849, 1850) and have proved to represent one of the definitive histological characters of the majority of genera in the Theaceae (Kochs 1900; Solereder 1908; Beauvisage 1920; Melchior 1925). Despite the frequent reference to these cells in general texts and in the scattered literature on "sclerenchyma," little is known about the details of their developmental history. Indeed, aside from the brief account given by Buch (1870), the investigations of Cavara (1897) appear to be the only effort to explore the origin and growth of these cells. Cavara, adopting a term originated by Sachs (1882), designated the isolated branched cells in *Camellia* as "idioblasts." He stated that the ramified character of the cell results from a true intercellular growth of the wall between neighboring tissue-elements during early phases of ontogeny. If Cavara's conclusion is correct, the idioblasts of *Camellia* should offer interesting material for a study of the much-disputed phenomena of "gliding" or "intrusive" growth (Majumdar 1941; Sinnott and Bloch 1939, 1943).

But in addition to their morphogenetic interest, the branched cells in the leaf of *Camellia* pose a further question, viz.: what is the morphological nature of such extraordinary cells? Reference to table 1 will show that eleven distinct histological terms have been applied to these elements. A discussion of this exceptionally confusing nomenclature must be postponed until the observational data in this paper have been presented. Here it is only essential to emphasize that this confusion in terminology is by no means restricted to *Camellia*. Cells which appear fundamentally similar at least in form to those in *Camellia* occur in a large number of angiosperm groups as well as in certain gymnosperms (Thomas 1865; Seward 1906; Solereder 1908). The nomenclature for these elements includes many of the terms listed in table 1. It is thus evident that the entire problem of so-called "sclerenchyma" merits careful re-examination. It is hoped that the present study may serve to stimulate and to orient intensive as well as extensive investigations in both angiosperms and gymnosperms.

* Plates 2 and 3 are published with the help of a contribution by the author and of the Lucien M. Underwood Memorial Fund.

For convenience and brevity, Tschirch's (1885) term "sclereid" will be employed in the descriptive sections of this paper. A brief account of the origin and applicability of this term to sclerenchymatous elements has already been given in a recent book by the writer (Foster 1942, p. 67–70).

MATERIAL AND TECHNIQUE

The leaves of *Camellia japonica* used for this investigation were collected from vigorous plants growing on the campus of the University of California at Berkeley. The horticultural variety represented by these plants could not be determined, however, because of the variable character of the flowers. For comparative purposes, a brief study was also made of the sclereids in the leaves of *Camellia reticulata* Lindl. and *Camellia sinensis* (L.) O. Ktze. Material of the later species was obtained from plants in Golden Gate Park, San Francisco, through the kindness of Mr. Eric Walther.

Preliminary study of hand-sections of the leaf of *C. japonica* showed that the sclereids are most abundant in the petiole. Consequently this portion of the leaf served as the basis for all developmental studies. Young as well as mature petioles were cut transversely into sectors and fixed for 24 hours in a mixture of formalin–acetic acid–ethyl alcohol according to a formula given by Sass (1940, p. 16). Dehydration, clearing with xylene, and infiltration with paraffin were carried out using the general procedure recommended by Ball (1941). Serial trans- and longisections 6–8 μ in thickness were easily secured from young petioles in which the sclereids are thin-walled. But for maturing and adult sclereids, it was necessary to soften the material. To accomplish this, a small portion of the tissue of the imbedded petiole was exposed by trimming away the paraffin and the block then immersed for 2–3 days in a solution of glycerine-alcohol (90 cc. 60 per cent alcohol; 10 cc. glycerine). By this method, thin and usually unscratched serial sections could be obtained with little difficulty. A modification of the tannic acid–iron chloride–safranin method was adopted for staining the sections (Foster 1934). This involved the use of a 0.5 per cent aqueous solution of tannic acid in which the slides were placed for five minutes before transfer to the iron chloride. The preparations were then washed thoroughly in running water and counterstained for 24 hours or less in safranin. This slight modification of the writer's previous method resulted in a sharp and pleasing color contrast between the walls of the parenchymatous tissues and the sclereids.

Macerated petioles were found indispensable for a study of the elaborate forms of the adult sclereids. The method of maceration outlined by Priestley and Scott (1938, p. 193–194) gave excellent results. Thick transverse sections of fresh petioles were first thoroughly aspirated in acid-alcohol (3 parts

70 per cent ethyl alcohol : 1 part concentrated HCl). New acid-alcohol was then added and allowed to act for 24 hours. After thorough washing in water the material was placed in a 0.5 per cent aqueous solution of ammonium oxalate. Within several days, the parenchyma tissues were sufficiently macerated to permit a ready examination of the isolated sclereids. Permanent glycerine-jelly mounts were made of both unstained as well as safranin-stained material.

Thanks are due the writer's wife, Helen Vincent Foster, for her skillful execution of the perspective drawings of the sclereids illustrated in figures 2–8. Acknowledgment is also made to Dr. Roger Reeve for his generous assistance in imbedding some of the materials used in this study.

DISTRIBUTION OF SCLEREIDS IN THE PETIOLE

When serial transverse sections of mature petioles are examined, it is evident that the sclereids do not form a continuous tissue but are scattered as typical idioblasts[1] in certain definable regions of the "fundamental tissue system" (fig. 1). Sclereids are most abundant in the outer cortical region where they collectively form a discontinuous cylinder of thick-walled polymorphic cells. The tissue in which they lie consists of relatively small cells with inconspicuous air-spaces. In transection these cells very closely resemble collenchyma because of the irregular thickenings of their walls (figs. 23–26). But in longisection the cells are short and cannot therefore be classified as "typical" angular collenchyma. The remainder of the fundamental tissue system is composed of larger thinner-walled parenchyma. Intercellular spaces are particularly well developed in the adaxial portion of this tissue which closely resembles in structure typical spongy parenchyma. While sclereids are found sporadically in the parenchyma near the phloem of the single collateral bundle, they appear more consistently in the midst of the large-celled parenchyma adjacent to the xylem (fig. 1, *ms*). In this pith-like portion, many of the sclereids are particularly large and thick-walled.

As is clearly indicated in figure 1, the greatest dimension of the "cortical" sclereids tends to lie parallel to the epidermis or to the contour of the vascular bundle. This is most clearly shown by the sclereids in the adaxial cortex which lie virtually at right angles to the longitudinal files of cells in which they are imbedded (fig. 26). The significance of this arrangement, which is markedly different from the vertical orientation of "typical" fibers, will appear when the ontogeny of the sclereids is described.

FORM OF THE MATURE SCLEREIDS

A thorough study of both serial sections as well as macerations reveals the remarkable polymorphism typical of the sclereids of *Camellia japonica*.

[1] Occasionally, isolated groups of 2–3 connected sclereids may be seen in following serial sections, but such "nests" scarcely represent a "tissue" (cf. fig. 20).

Cavara (1897) attempted to show that the form of the sclereid is to some extent correlated with its position in the leaf. According to his descriptions, profusely branched forms occur in the parenchyma surrounding the vascular bundle in the petiole and midrib while in the lamina Y-, L-, and T-shaped forms prevail. In the writer's experience, such a distinction cannot be drawn and virtually all of the "form-types" recognized by Cavara may occur in the parenchymatous tissue of a single petiole.

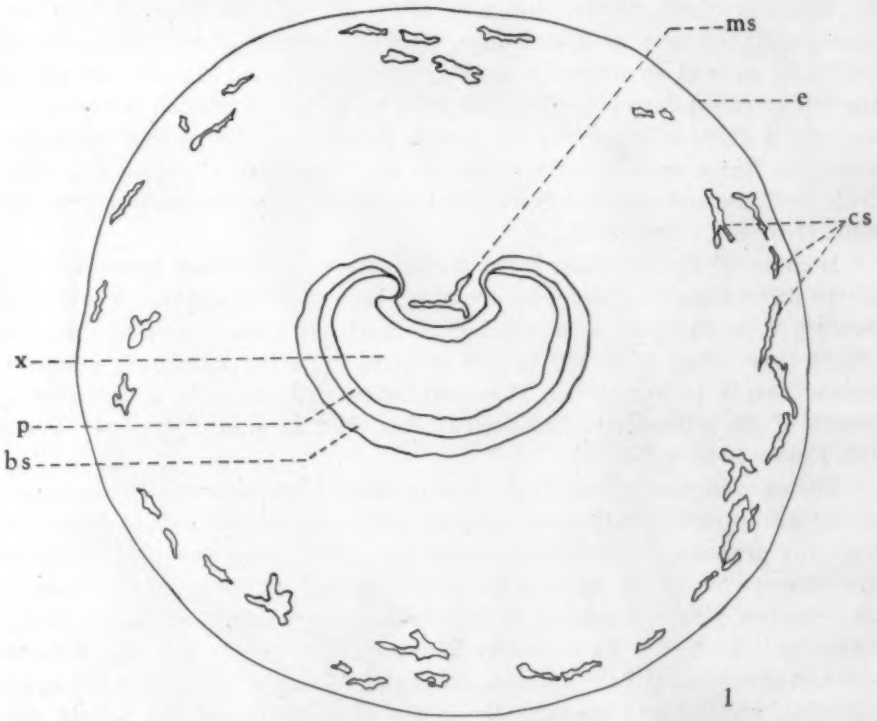

FIG. 1. Transection of the petiole of *Camellia japonica* showing the distribution of the sclereids as idioblasts in the "fundamental tissue system." This illustration was prepared by first tracing in ink the outlines of the epidermis, sclereids and vascular tissues on a photomicrograph which was then placed in a solution to remove the photographic image. Legend: *bs*, bundle sheath; *cs*, sclereids of outer cortex; *e*, epidermis; *ms*, medullary sclereid; *p*, phloem; *x*, xylem. ×45.

Because of the bewildering intergradations in form, it is only possible to point out some of the most commonly recurring form-types. Many sclereids are fusiform and, except for their peculiar oblique or transverse orientation with reference to the long axis of the petiole, resemble in their general form short fibers (figs. 5, 26). Very commonly however the sclereid is branched, often in a most curious fashion. In the simpler type of branching, the cell is roughly Y-shaped with either symmetrical or asymmetrical

arms (figs. 7, 8). In a not infrequent type, the cell is extended in length and provided at one or both ends with a pair of short divergent branches (fig. 6). The most bizarre configuration however is presented by the varied "stellate" types (figs. 2, 3, 19, 23, 24, 25). Such cells consist of a thick central portion from which four or more arms radiate. When the branches are relatively equal and lie nearly in the same plane, the cell might appropriately be designated as an "astrosclereid," following the nomenclature proposed by Tschirch (1885, 1889). But very often cells of this general type are extremely grotesque in appearance, because certain of the arms extend vertically as well as obliquely from the central region (fig. 3). As far as the writer could determine there appears to be no correlation between the form of a given sclereid and its specific position in the petiole. Although branched forms seem to predominate in the "medullary" region (fig. 19), both fusiform and elaborately ramified types occur indiscriminately in the outer "cortex" (figs. 23–26).

Because of the irregular form of the sclereids, accurate measurements of the dimensions of these cells are often impossible to obtain. A series of random measurements of a number of fusiform types indicates that the length may range from 250 to 530 microns while the maximum diameter varies from 20 to 35 microns. These data show that the ratio of diameter to length of the sclereids is considerably less than in many "typical" fibers (cf. Foster 1942, p. 74–75).

The examination of hundreds of cells isolated by maceration reveals one of the most striking and consistent peculiarities of the sclereids of *Camellia*, viz.: the presence of numerous, short, conical or irregular protuberances distributed irregularly on both the main "body" of the cell as well as on its branches. For convenience in description, these processes will be designated as "spicules." As is clearly illustrated by figures 2–8, the relative size and abundance of the spicules are highly variable. Certain of the small sclereids, which occur sporadically in the outer cortex of the petiole, are relatively smooth-walled (figs. 4, 8). But the spicules are often so numerous and closely-spaced on the larger sclereids that such cells have a distinctly "spiny" appearance (figs. 2, 3, 5, 6, 7). Despite the many allusions to the sclereids of *Camellia* in botanical literature, it is a noteworthy fact that the only reference to the distinctive spicules is made by Cavara (1897), probably because he made a careful study of elements isolated by maceration. Neither Kochs (1900), Solereder (1908), Beauvisage (1920), nor

Explanation of plate 2, figs. 2–5

FIGS. 2–5. Camera lucida drawings of adult sclereids isolated by maceration. FIGS. 2, 3. Stellate types. FIG. 4. Weakly-branched type. FIG. 5. Fusiform type. Note the characteristic spicules and the narrow lumina in figures 2, 3, and 5; only a few of the numerous pit-canals are shown. In figure 4, the lumen is broader and few spicules are present. All figures × 236.

FOSTER: SCLEREIDS IN CAMELLIA

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FOSTER: SCLEREIDS IN CAMELLIA

Melchior (1925) in their anatomical treatments of the tea family refer to the spiculate character of the sclereids. Indeed Melchior (p. 111, fig. 59) simply repeats the familiar figure copied from Tschirch (1889, p. 304, fig. 348) which depicts branched sclereids of *Thea* in sectional as well as isolated view with "smooth" walls. For comparative purposes, the writer made a study of the adult sclereids in the petioles of leaves of *C. reticulata* and *C. sinensis*. In both of these species, the isolated sclereids closely resemble those of *C. japonica* in their form and noticeably spiculate character.

As will be shown later, the spiculate character of the sclereid is acquired during the early ontogeny of the cell as a result of local and restricted extensions of the primary wall. Thin transverse sections of nearly mature sclereids clearly show that the majority of the spicules are truly intercellular, extending for short distances into the middle lamella between adjacent parenchyma cells (fig. 26). Because of such numerous projections, which subsequently develop secondary walls, the sclereid evidently is firmly "anchored" to the tissue-elements which surround it. Spicules also may extend freely into air-spaces which lie near the extensible primary wall of the sclereid (figs. 19, 21, 22, 29). These spicules are readily seen, even in comparatively thick hand-sections of the petiole and it is therefore difficult to see how they were overlooked by such early workers as Buch (1870).

ORIGIN AND DEVELOPMENT OF SCLEREIDS

Despite the varied form-types exhibited by the adult petiolar sclereids, these cells originate from parenchymatous elements of the "fundamental tissue system." This fact is essential to a clear understanding of the remarkable ontogeny of the sclereid. In agreement with Cavara's (1897) observations, the sclereid initials are not morphologically recognizable until the foliage leaf has emerged from the bud and is beginning its final phase of expansion and maturation. In the variety of *Camellia japonica* used in this study, sclereid initials are first evident in leaves 5–6 centimeters long. At this stage, the petiole has reached nearly its full length although it is slightly smaller in diameter than that of the adult leaf.

What criteria distinguish a sclereid initial from neighboring parenchymatous elements? In view of the idioblastic distribution of the initials in both large- and small-celled tissue, it is obvious that neither relative size nor position is a definitive character. According to Cavara (1897, p. 79), the large size of the nucleus clearly demarcates a young idioblast from

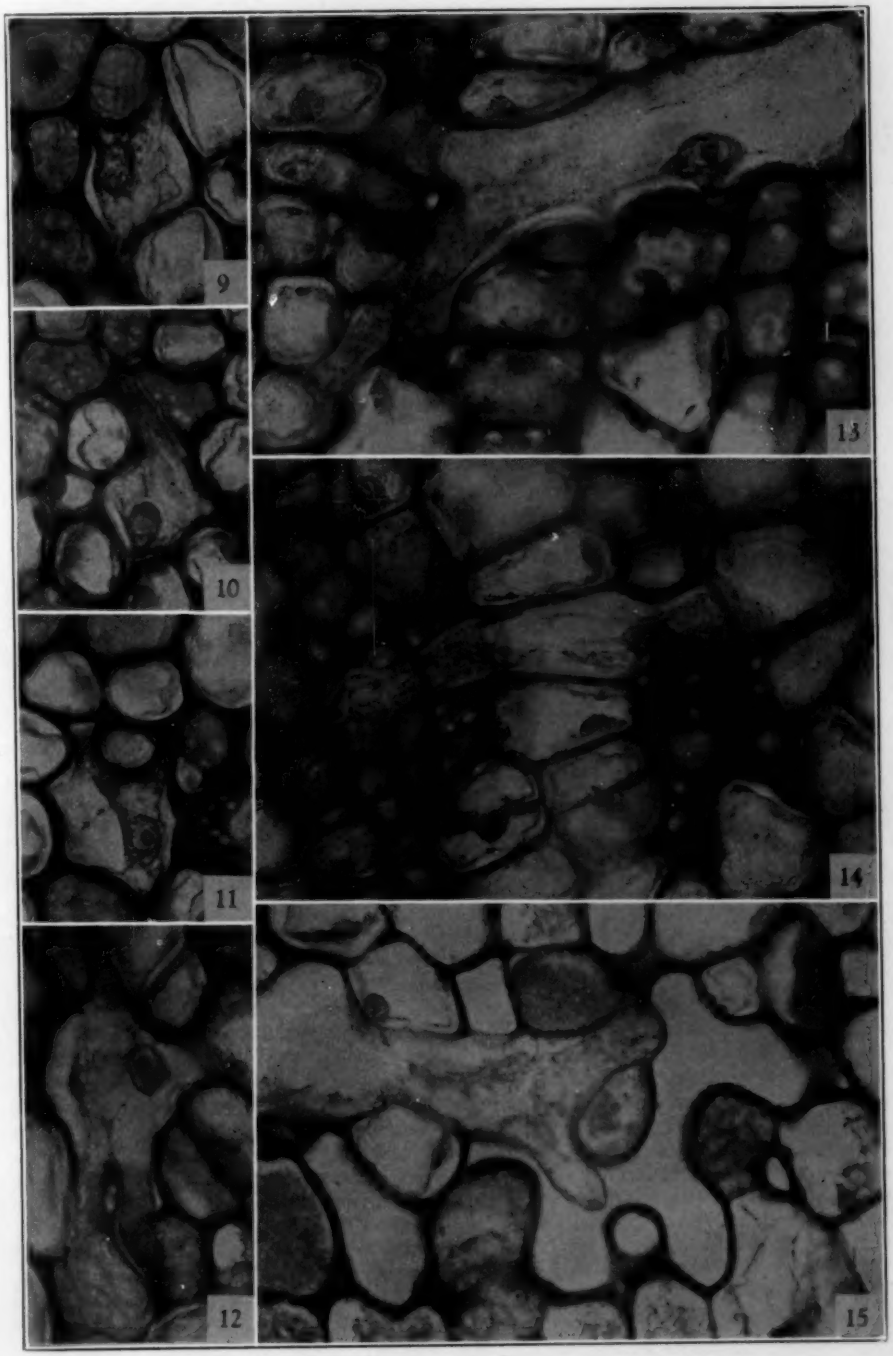
Explanation of plate 3, figs. 6–8

FIGS. 6–8. Camera lucida drawings of sclereids isolated by maceration. FIG. 6. Elongated type with dichotomous tips. FIGS. 7, 8. Y-shaped types. Note the abundant spicules and the very narrow lumina of the cells in figures 6, 7. In figure 8, the lumen is broad and the surface of the cell nearly smooth. All figures × 236.

neighboring cells. This conclusion is supported by the present study, and reference to figures 9, 10, and 12 will show the striking size difference between the nuclei of young sclereids and their neighboring tissue-elements. Cavara found that the nuclei of young idioblasts are "14–16 microns in length and 10–14 microns in width while the nuclei of surrounding cells measure only 6–8 microns by 4–6 microns." He further stated that the nucleus of the young idioblast is also distinguished by a prominent central "globular body." The latter is highly-refractive in living nuclei and in his view is not the nucleolus because it is vividly colored by "achromatic stains." The writer's observations on fixed as well as living material confirm the existence of a prominent, more or less centralized body in the nucleus of actively growing sclereid-initials (figs. 9–14). But in many instances the nucleus may exhibit as many as three distinct "central bodies," which superficially at least appear to be nucleoli. No final decision, however, is possible until a thorough study of metabolic and dividing nuclei in the various leaf tissues of *Camellia* has been undertaken.

By utilizing the distinguishing character of nuclear size it is possible to study the walls of sclereid initials prior to the enlargement of these cells. With the techniques used in this investigation, the walls of the initials appear essentially similar to those of the surrounding parenchyma cells. This is particularly evident in the outer cortex of the petiole where the thickened areas of the walls of both cell types exhibit typical primary pit-fields (figs. 9–12). It is therefore clear that the irregular growth of the sclereid as an idioblast must depend first of all upon the ability of its wall to distend at certain points. Careful examination of hundreds of cells shows that the distensible regions invariably occur at the corners where the initial is in contact with the middle lamella separating two adjacent parenchyma cells.

Figures 9–12 illustrate very early stages in the growth of sclereid initials in the cortex of the petiole. In each it is clear that the initial has produced one or more slender delicate, tubular branches which extend between the walls of neighboring tissue elements. As mentioned earlier in this paper, the outer cortical cells exhibit collenchymatous thickenings when viewed in transection. Hence, as is shown in figures 9 and 11, the early tubular extensions of the sclereid must literally force their way through such thickened areas. Whether this is accomplished by the secretion of specific pectin-digesting enzymes, as appears to be the case for many pollen tubes (Paton 1921), remains to be proved. At any event it seems true that the ramification of the sclereid represents true intercellular development. No evidence has been found of either crushed primary walls in invaded parenchyma tissue nor of the penetration of parenchyma cells by the arms of the sclereid.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In some instances, the initial at first produces a single tube-like process which may often be seen in "broad view" directly in contact with one of the primary walls of an adjacent parenchyma cell (fig. 10). Initials observed in this plane of section suggest that the growing tubular-arm does not "avoid" the primary pit-fields between two parenchyma cells. Indeed, it is difficult to imagine how the pit-fields with their plasmodesmata can fail to be split apart at certain regions of the wall. Very commonly, tubular branches arise at two adjacent corners of a sclereid initial. This results in a dichotomous branch between the two arms of which lies a parenchyma cell (figs. 9, 11, 12). The continued development of a dichotomous branch leads to the Y-type of adult sclereid while the formation of additional dichotomies from other corners of the initial results in stellate or irregularly branched types (figs. 2, 3, 7, 8).

Further development of the sclereid involves the gradual enlargement of the main body of the cell and the continued intercellular growth of its tubular branches. As the latter increase in length, their course often becomes so irregular that they cannot be seen as entire structures either in trans- or longisectional view. Cavara's (1897, pl. XXXI, fig. 8) illlustration depicts a young stage and gives no idea of the extraordinary undulation and growth in various planes of the arms of branching sclereids. Occasionally, a developing tube may pursue a fairly regular intercellular course because of the more or less regular arrangement of the parenchyma cells in its path (fig. 14). But more frequently, one or more of the arms of a sclereid grow vertically or obliquely with reference to the main body. This has been observed convincingly in longisection (fig. 13) and is readily deduced from the incomplete transections which are usually obtained of advanced stages in sclereid ontogeny (figs. 16, 17).

The behavior of the intercellular branches of sclereids in lacunate areas of the parenchyma is particularly interesting. In the relatively compact

Explanation of figures 9–15

FIGS. 9–12. Transections of early stages in intercellular growth of sclereid initials. Note the large nucleus with its prominent nucleolus in each young sclereid. FIG. 9. An initial with three short tubular branches. FIG. 10. "Broad view" of a tubular branch in contact with the primary wall of a parenchyma cell; note the pit-fields (light areas) in the latter. FIG. 11. An initial with two short intercellular branches. Note the pit-fields seen in section view in the wall of this initial and the typical collenchymatous thickenings of neighboring parenchyma cells. FIG. 12. An initial showing dichotomous branching at lower side. This is also illustrated in figures 9 and 11. FIGS. 13, 14. Longisections of older stages in intercellular development of sclereid initials. FIG. 13. Initial with long, oblique branch the tip of which (lower left) is dichotomous. Note abundant cytoplasm in this branch and the large solitary nucleus. FIG. 14. Initial with delicate branch extending nearly at right-angles to vertical files of parenchyma cells. Note the development of two spicules from the lower wall of the initial at either side of the prominent nucleus. FIG. 15. Transection of the dichotomous branch of a sclereid initial at its point of entrance into a prominent air-lacuna. Note the tenuous character of the primary wall. All figures ×550.

tissue of the outer cortex, the delicate tips of certain of the sclereid branches have been observed to extend freely into small air-spaces. Better examples, however, are provided by those sclereids which originate and develop in the more loosely-arranged parenchyma of the inner cortex and the pith. In these regions, the growing tips of the branches very frequently enter the large intercellular spaces. A striking illustration is shown in figure 15, which depicts the dichotomous end of a young sclereid just penetrating a very conspicuous air-lacuna. Buch (1870, p. 28), who apparently confined his observations to developing sclereids in the mesophyll of the lamina, states that the branch of a sclereid grows freely into an intercellular space "until it fills it completely." Such a phenomenon has never been observed by the writer in the petiole of *Camellia*.[2] On the contrary, soon after its entrance into a lacuna, the extension of the tip of the tube ceases. At maturity, such intrusive tips may be seen to occupy only a portion of the intercellular lacuna (fig. 21).

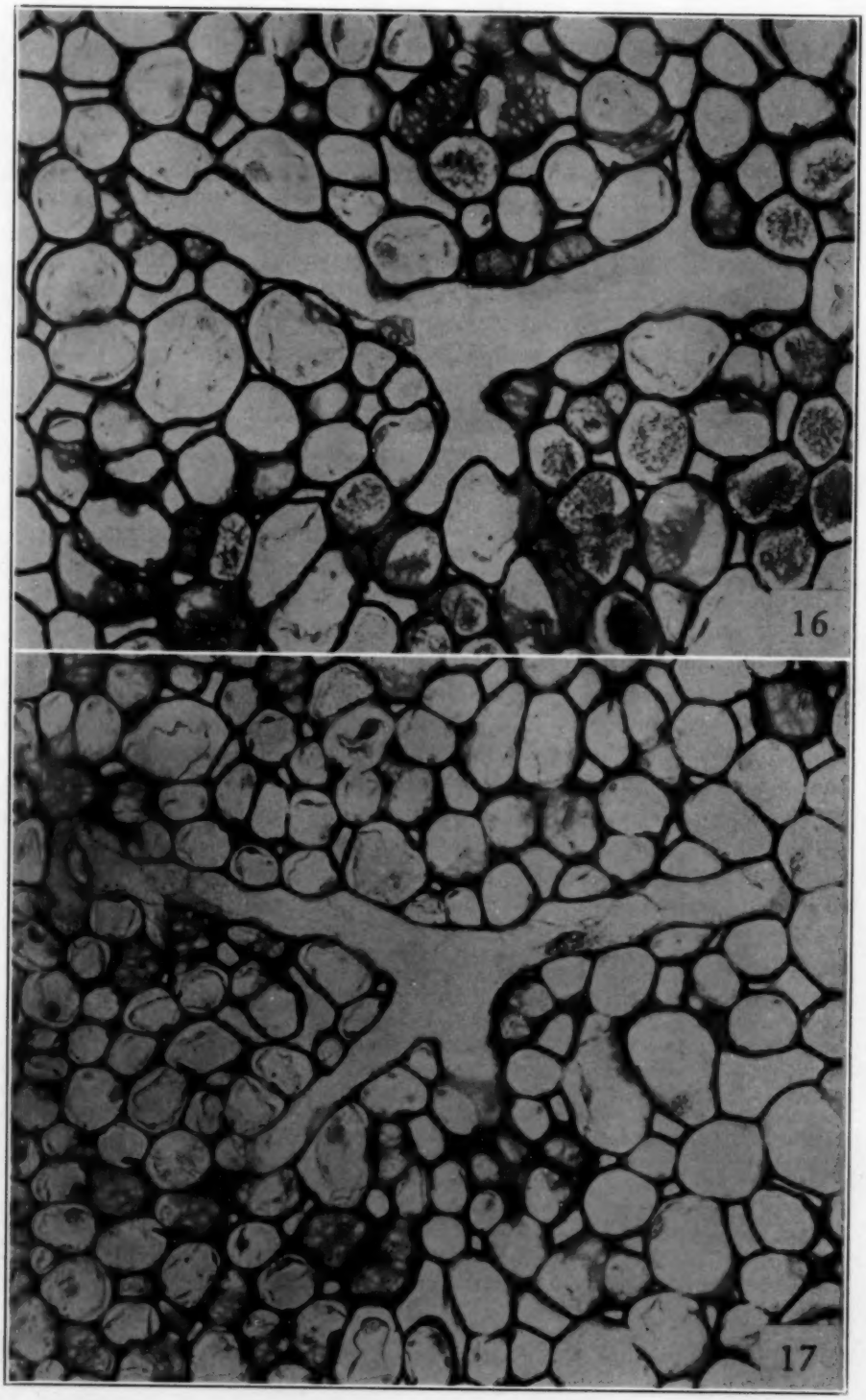
The markedly extensible nature of the primary wall of young sclereids is very clearly illustrated by the development of the characteristic spicules which have been described earlier in this paper. From an ontogenetic standpoint, these structures represent "minor branches" of the cell and only differ in degree of development from the "major branches." Spicules originate during the formation of the major branches and like them are truly intercellular in their growth. As is shown in figures 13 and 14, young spicules appear as short conical protuberances which extend between the walls of certain of the parenchyma cells bordering on the main body of the sclereid and its branches. As is true of the main branches of a sclereid, the tips of the spicules may enter intercellular air spaces (figs. 19, 21, 22, 26). The factors which determine the frequency of intercellular outgrowths and hence the number and distribution of spicules on the mature sclereid are unknown. But it is interesting that the small and presumably less vigorously developing sclereids typically exhibit relatively few spicules (cf. figs. 4, 8). This suggests that wide differences in the physiology of wall growth may exist between sclereids occurring in the same general region of the petiole.

As far as the writer could determine, the protoplast remains uninucleate

[2] According to Buch (1870, p. 16–18), the remarkable H-shaped sclerenchyma cells in the petiole of *Fagraea auriculata* (Loganiaceae) owe their form to the development of parallel "arms" *within* the vertical air-spaces bordering the cell. Buch compares these cells and their development with the apparently similar elements found in the aerial roots of *Monstera Lennea* (cf. also the statements by Solereder 1908, p. 539–540).

Explanation of figures 16, 17

Transections of large ramified sclereids at the close of the period of intercellular growth. With the exception of the short pointed spicule at the upper right of figure 16, none of the tips of the branches are in the plane of section. Note the variation in the relative position of the prominent nucleus in each sclereid. ×380.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throughout the entire intercellular growth of the sclereid (figs, 9–14, 16, 17). This contrasts markedly with the multinucleate condition which arises during the extension of certain bast fibers (Esau 1938, 1943). Because of the irregular form which is acquired early by the developing sclereid, interpretations based on serial sections may be open to question. To eliminate this objection, thin slices of petioles were fixed in absolute alcohol–acetic acid, macerated in 50 per cent hydrochloric acid, and smears stained in aceto-carmine. A single large, weakly chromatic nucleus was observed in all immature sclereids which were suitable for study by this technique. During the late phases of secondary-wall formation, the sclereid likewise appears uninucleate (figs. 26, 27, 29–32). According to Puchinger (1923) a single lens-shaped nucleus with two nucleoli is present in the mature sclereids of leaves of *Thea japonica*. Her observations indicate that the sclereids retain their nuclei for as long as three years.

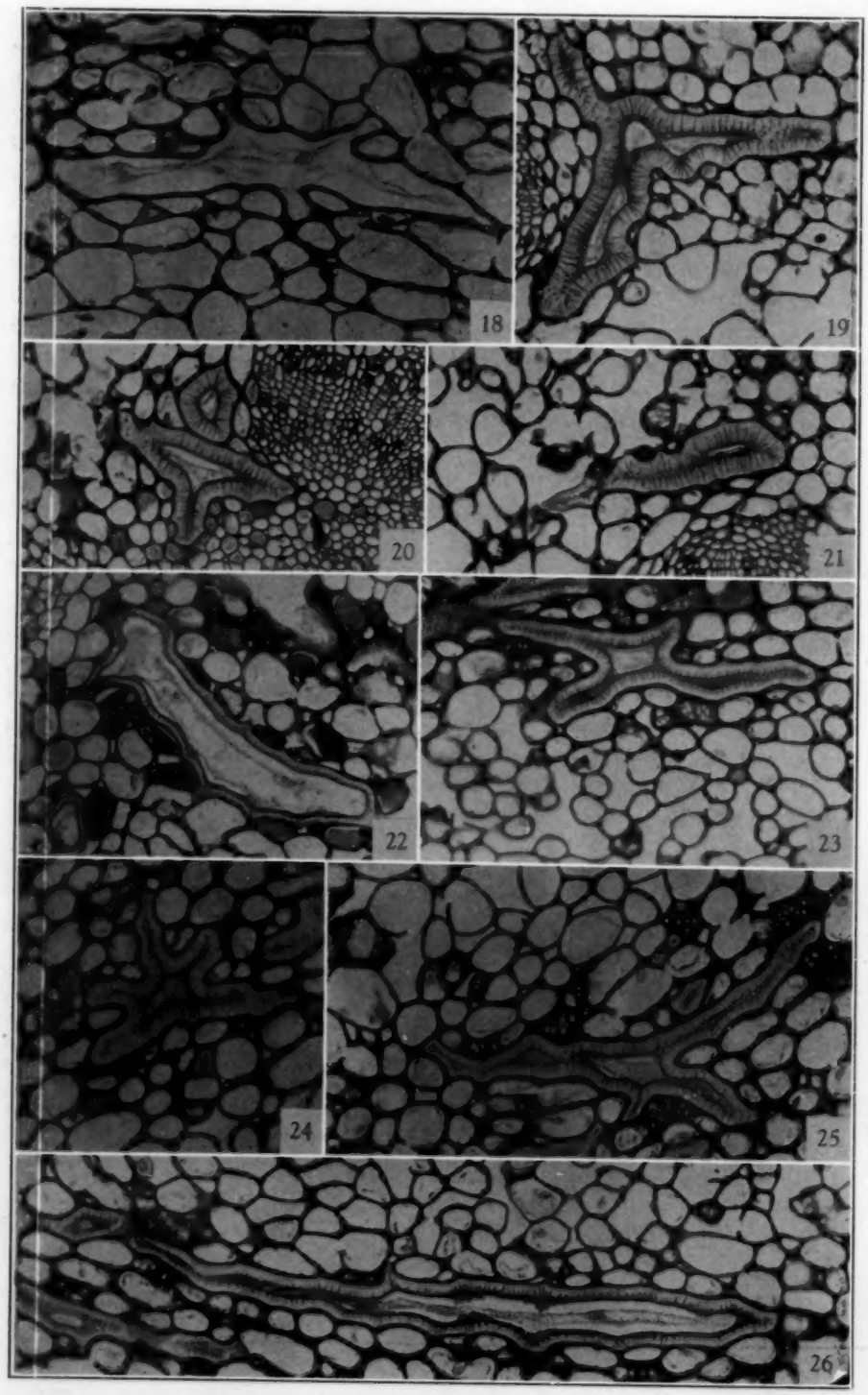
DEVELOPMENT OF THE SECONDARY WALL AND PIT CANALS

During its phase of enlargement and intercellular growth, the sclereid is provided with a thin primary wall. The extremely tenuous nature of this membrane is clearly shown when the intercellular branching of the initial begins as well as in certain favorable sections of older tubes (figs. 9–14). Exceptionally clear views of the primary wall are also obtained at the points of entrance of the delicate ramifications of a sclereid into air-lacunae (fig. 15). When enlargement ceases, the sclereid rapidly acquires a massive secondary wall which may develop to such an extent that the lumen becomes occluded or reduced to a narrow channel, particularly in the branches (figs. 2, 3, 5, 6, 7).

Although the irregular form of the sclereid makes interpretation very difficult, it is probable that secondary wall formation is initiated uniformly

Explanation of figures 18–26

FIG. 18. Transection of ramified sclereid from cortex showing an early stage in the development of the secondary wall. Note the shrunken cytoplasm and the single nucleus. FIGS. 19–22. Transections of sclereids from the pith region of the petiole. FIG. 19. Large branched type with thick secondary wall and abundant ramiform pit-canals. Note the extension of spicules into air-spaces at the lower right and center of this cell. FIG. 20. Two sclereids in contact, the upper represented by a branch shown in transection. A portion of the vascular bundle appears at the right of these sclereids. FIG. 21. Sclereid with tip lying free in an air-lacuna. Note spicules at upper edge of this cell. FIG. 22. Sclereid, showing early stage of secondary wall and pit-canals. Observe the prominent spicules of this cell, some of which extend into air-lacunae. FIGS. 23–26. Transections of sclereids from the cortex of the petiole. FIG. 23. Branched type, showing numerous and closely-spaced pit-canals. FIG. 24. Stellate type, showing pit-canals in the thick secondary wall. FIG. 25. Large, irrgeularly branched type. Note the conspicuous pit-fields (light areas) in the walls of adjacent parenchyma cells. FIG. 26. Fusiform type, comparable in general form to the cell shown in figure 5. Note the solitary nucleus, the numerous pit-canals and the prominent spicule (upper edge, near center). All figures $\times 190$.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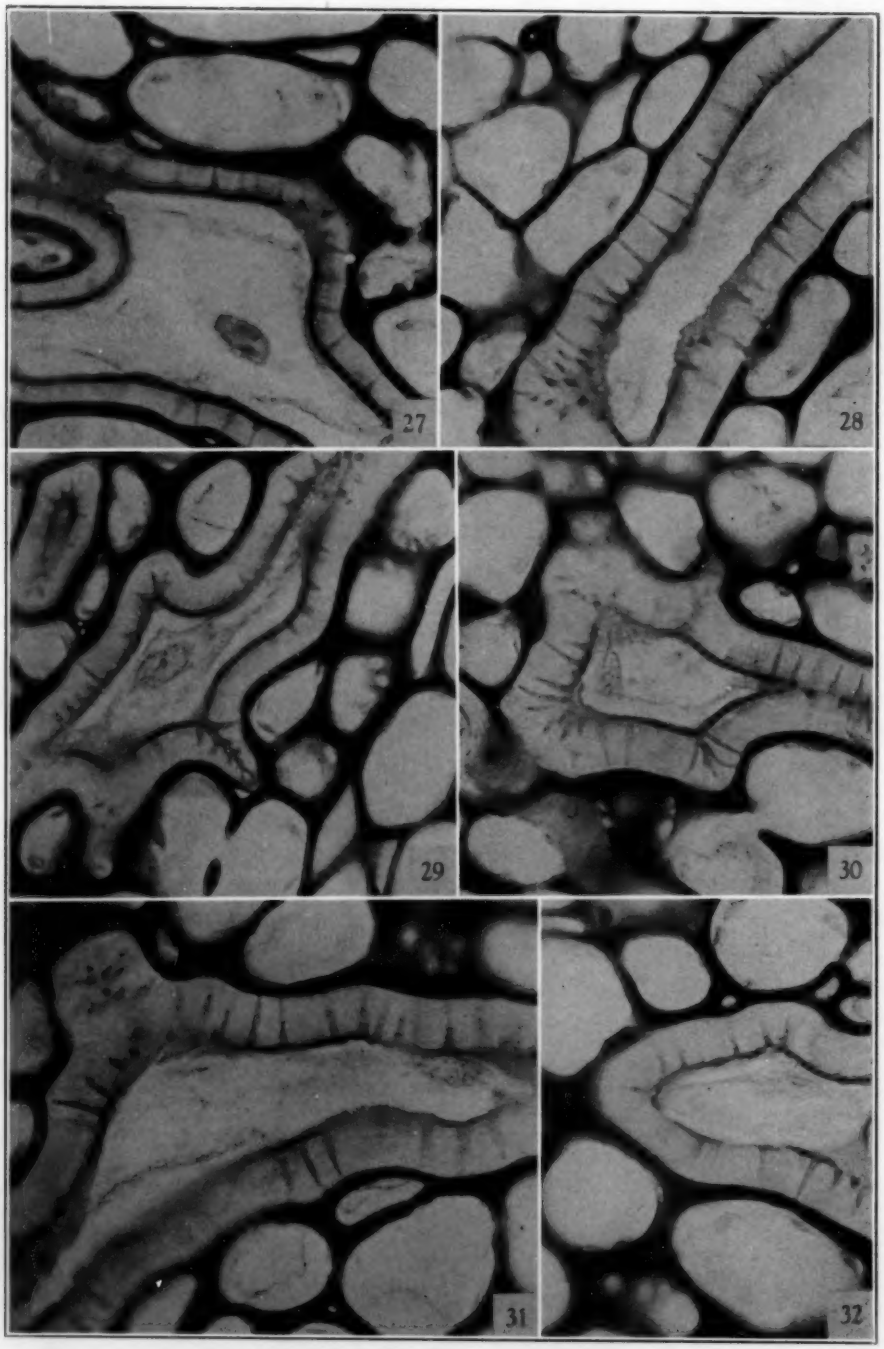
throughout the entire cell. When first recognizable, the young secondary wall is stained a brilliant red with safranin and thus is sharply demarcated from the purplish-blue primary walls of the adjacent parenchyma cells (fig. 18). At this stage, the secondary wall is provided with small shallow pits which are sparsely and unevenly distributed. But as the centripetal deposition of the wall continues, the characteristic pit-canals make their appearance and become increasingly evident and numerous. At maturity, the secondary wall is penetrated by very numerous, slender and often ramified canals which impart a distinctive character to the sclereids of *Camellia* (figs. 19–26).

The investigation of the origin and development of the pit-canals from the simple pits is difficult because the former are so frequently oriented obliquely with reference to the plane of section. As a result, extensive areas of the secondary wall may appear to be traversed by "short" canals which fail to extend to the primary wall of the cell (figs. 23, 26). Furthermore where ramified canals occur, many of the "branches" curve out of the plane of section and thereby produce characteristic effects which are difficult to interpret (figs. 19, 24). It seems clear that the failure to recognize adequately these difficulties is largely responsible for Cavara's (1897, p. 73–74, pl. XXXI, figs. 17–21) description of canal development. He states: "These canals at first are 2.5 microns apart, they are circular in section and .05–.08 microns in diameter. Their arrangement is spiral and very regular, as can be seen in profile. *As the wall thickness increases, the canals increase in number, new ones intercalating themselves between previous ones through new plates of thickening.*" (Italics mine.)

The present investigation furnishes no support for this interpretation. If Cavara's view were correct, the intercalation of new canals between older ones would obviously require some type of centrifugal penetration of the *secondary wall* by cytoplasmic extensions. Careful examination of young stages provides no evidence for such an assumption. When thin serial sections are compared, it becomes evident that the "new" canals described

Explanation of figures 27–32

Transections of portions of the secondary wall of cortical sclereids to show details of pit-canals. FIG. 27. Young stage in secondary-wall development. A completely-sectioned pit-canal is paired with a primary pit-field at the upper edge of the sclereid. FIG. 28. Section illustrating the oblique course of the canals in the secondary wall. Pairing between pit-fields and pit-canals is shown at left and right near the base of the sclereid. FIG. 29. Illustrating the ramiform pit-canals in a prominent spicule (lower right). Note that a curved canal in the spicule is paired with a pit-field in the adjacent parenchyma cell. FIG. 30. Illustrating ramiform pit-canals (lower edge), and spicules. Two of the canals lie opposite corresponding pit-fields. FIG. 31. Showing two perfectly bisected pit-canals at upper edge of sclereid, and the corresponding pit-fields in the parenchyma cell. FIG. 32. Showing two completely sectioned pit-canals (lower edge). Note the small circular chambers and the pit-membranes. All figures × 550.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by Cavara merely represent the *inner* portion of canals which run obliquely through the entire thickness of the secondary wall. A striking example is furnished by figure 28. At the lower left of the sclereid, the characteristic curved and oblique course of the canals is very evident. Just above this region, a series of four canals may be seen, of which only one extends completely through the wall and coincides with the pit-field of the adjacent parenchyma cell. The other three canals clearly extend at successively more oblique angles, culminating in the short and "incomplete" canal at the top of the series.

Since the sclereids typically develop as idioblasts, the question naturally arises as to the relationship between their very numerous pit-canals and the "sieve pitting"[3] on the contiguous walls of parenchymatous elements. As stated earlier in the paper, there is good reason for believing that the intercellular extension of the primary wall of the sclereid results in the splitting apart of certain of the paired primary pit-fields between the parenchyma cells lying in its path. Under such circumstances, one might expect that the pit-canals would coincide in position with some (all?) of the separated members of the originally paired pit-fields. This can be demonstrated in many instances and is not surprising in view of the well-developed character of the sieve-pitting of the parenchyma cells. In figures 27–32, one or more entire pit-canals coincide with primary pit-fields in adjacent parenchyma cells. This relationship is particularly well shown in figures 29 and 32 where the delicate membranes separating the pit-chambers from the pit-fields are clearly seen.

In sectional view, a pit-canal consists of a cone-shaped channel extending from the inner surface of the secondary wall to the small circular pit-chamber. The latter is slightly overarched by the secondary wall and hence may be designated as "bordered" (figs. 27–32).

Extensively "branched" pit-canals develop at various regions of the wall and are particularly well-shown in all of the larger spicules (figs, 19, 21, 22, 26, 29, 30). A study of their ontogeny shows that the "main channel" represents the lateral extension of the lumen into the spicule while the "branches" are a series of originally separate canals which coalesce with the former during secondary-wall thickening. As is shown in figure 19, such ramiform canals are often very complex and difficult to interpret. In the simpler cases, however, it is possible to see that some of the lateral canals are paired with pit-fields in the adjoining parenchyma cell. Often this is associated with a remarkable degree of curvature of the canals (figs. 29–30).

An intensive study of the structure and chemical composition of the sec-

[3] This term is used to designate collectively the numerous primary pit-fields with their plasmodesmata which occur in the *primary* walls of parenchyma cells (cf. Bailey and Faull 1934, p. 241–243).

ondary wall of the sclereid has not been attempted. Nevertheless it is noteworthy that throughout its development as well as in its mature condition, the wall appears "homogeneous," i.e., non-stratified. This contrasts markedly with the easily visible lamellae in the secondary wall of the brachysclereids in the fruit of *Pyrus* and the pith of *Hoya carnosa*.[4] When sections of living petioles of *Camellia japonica* are treated with phloroglucin and hydrochloric acid, the thick walls of the sclereids become red. I–KI produces a bright lemon color. The reaction of the wall to these reagents is suggestive of the presence of "lignin." Cavara (1897) emphasized that as soon as the wall begins to thicken, it assumes a lignified character. His microchemical tests showed that the degree of lignification decreases *inwardly* in the wall, the innermost lamella giving the cellulose reaction with iodine and sulphuric acid. A careful investigation of the physicochemical make-up of the wall with modern techniques seems highly desirable. This might reveal the presence of non-cellulosic lamellae such as Bailey and Kerr (1935, p. 279–280) have discovered in the walls of sclereids in a number of angiosperms.

DISCUSSION

The present investigation has called attention to the many remarkable aspects of the development, form, and adult structure of the sclereids of *Camellia japonica*. The data may now be discussed most conveniently under two main topics, viz.: (1) the development of the sclereid as an idioblast, and (2) the problem of classifying the sclereid from a morphological standpoint.[5]

Idioblastic Development. Unlike the development of many tissue elements which maintain contacts with *all* their neighbors during differentiation, the ontogeny of the sclereid in *Camellia* involves notable changes in the original intercellular relationships of this cell. Beginning its existence as an idioblast in the parenchyma, the sclereid produces delicate tubular processes which "intrude" into the adjacent tissue and may even extend freely into air-spaces (figs. 9–15). It is very clear that the direction of growth of these tubular branches does not coincide with the short vertical elongation of the petiole. On the contrary, branching occurs in the most varied planes and often is oblique or nearly transverse to the longitudinal files of short parenchyma cells surrounding the sclereid (figs. 13, 14). Evidently, therefore, the extension of the sclereid is not explainable in terms of

[4] Buch (1870, p. 17) observed that the thick walls of the elaborately branched sclerenchyma cells of *Fagraea auriculata* exhibit a clearly laminated structure. The writer was able to confirm this observataion in a study of macerated elements of a petiole of *Fagraea* secured from the herbarium of the University of California.

[5] The writer acknowledges with thanks the many helpful discussions on "sclerenchyma" with Professor I. W. Bailey.

Priestley's (1930) theory of "symplastic growth." For this reason and also because there is no evidence of intracellular growth by the ramifying sclereid, it seems clear that true intercellular development must occur.

Although this conclusion appears inescapable, many difficulties arise when one attempts to visualize the "mechanics" of this type of idioblastic development. Does a considerable portion of a tubular branch of a young sclereid literally "glide" or "slip" over the walls between two neighboring protoplasts? Or, is elongation strictly limited to the very tips of the sclereid branches?

The latter type of growth movement in plant cells has been termed "intrusive growth" by Sinnott and Bloch (1939), who consider that true sliding growth "is rare or absent in most plant tissue and cannot be regarded as an important factor in development." Majumdar (1941, p. 170) reaches an essentially similar conclusion with respect to the fusiform initials of cambia and certain fibers. In their recent study of the development of the fibrous net in *Luffa cylindrica*, Sinnott and Bloch (1943, p. 98) state: "That the growth of the *Luffa* fibers is chiefly at their ends is indicated by the much thinner walls there. The two halves of a pit are always opposite each other, showing that there is no gliding after the pits are formed."

Because of the limitations of present technique, it is apparent that the evidence in favor of either "gliding growth" or "intrusive growth" is necessarily indirect. This will be true until methods have been devised for the direct observation of internal differentiating cells. Furthermore, the distinction between these two types of growth movements appears to be one of degree rather than of kind. For example, it seems clear from Bailey's (1923, p. 502–505) investigations that rather extensive wall elongation occurs during the increase in girth of non-stratified cambia. In such tissue, according to Bailey "the fusiform initials elongate, sliding by one another, until they attain a certain size." In contrast the fusiform initials of stratified cambia "divide radio-longitudinally and the products of such divisions expand laterally, but they do not elongate to any considerable extent." These differences in the degree of intercellular growth of cambial initials seem analogous to the various degrees of branching of the sclereids in *Camellia*. In the development of the "major branches" of a sclereid, elongation of considerable portions of the primary wall seems entirely possible. On the other hand, the growth of the characteristic spicules is more limited and very probably represents "intrusive growth." Vöchting (1908), in his classical treatise on morphogenesis, paid much attention to the bizarre types of idioblastic sclereids which were produced in great abundance in the tumors on leaf-bases of kohlrabi. With reference to the development of the sclereids Vöchting states (p. 192): "It is without further explanation clear that the penetration of the processes between the neighboring cells can only

be visualized by means of 'gliding' growth, which, as one sees in our tumors as well as in wound-tissue and other places in the plant, is of wide distribution." (Cf. also Küster 1935, p. 553–554.)

Whether the branched sclereids in *Camellia* are produced by "sliding" or "intrusive" growth, it seems evident that some of the original pairs of pit-fields, with their protoplasmic connections (or contacts) must be split apart. As discussed earlier in this paper, the slender and often ramified pit-canals of the sclereid are laid down opposite certain of the separated pit-fields of adjacent parenchyma elements (figs. 27–32). It has not been possible, however, to determine the effects of intercellular growth upon the middle lamella through which the tubular branches must penetrate. Since Kerr and Bailey (1934) have shown that the middle lamella is amorphous and plastic in character in young tissue, it is possible that the tubes "digest" their way between cells by the secretion of enzymes which act both chemically and physically upon polyuronides (cf. Paton 1921). This possibility of course needs to be tested experimentally.

Morphology of the Sclereid. The difficulties which arise in any attempt to classify morphologically the varied cell types in plants have been discussed recently by the writer (Foster 1942, p. 32–43). While it is relatively easy to demarcate the extremes in cellular specialization, frequent intergradations in form, wall structure, pitting, etc., occur and preclude rigid categories. The cells considered in this paper furnish a good illustration of the problems, because eleven more or less distinct terms have been applied to them since their discovery (table 1). When the various terms are examined

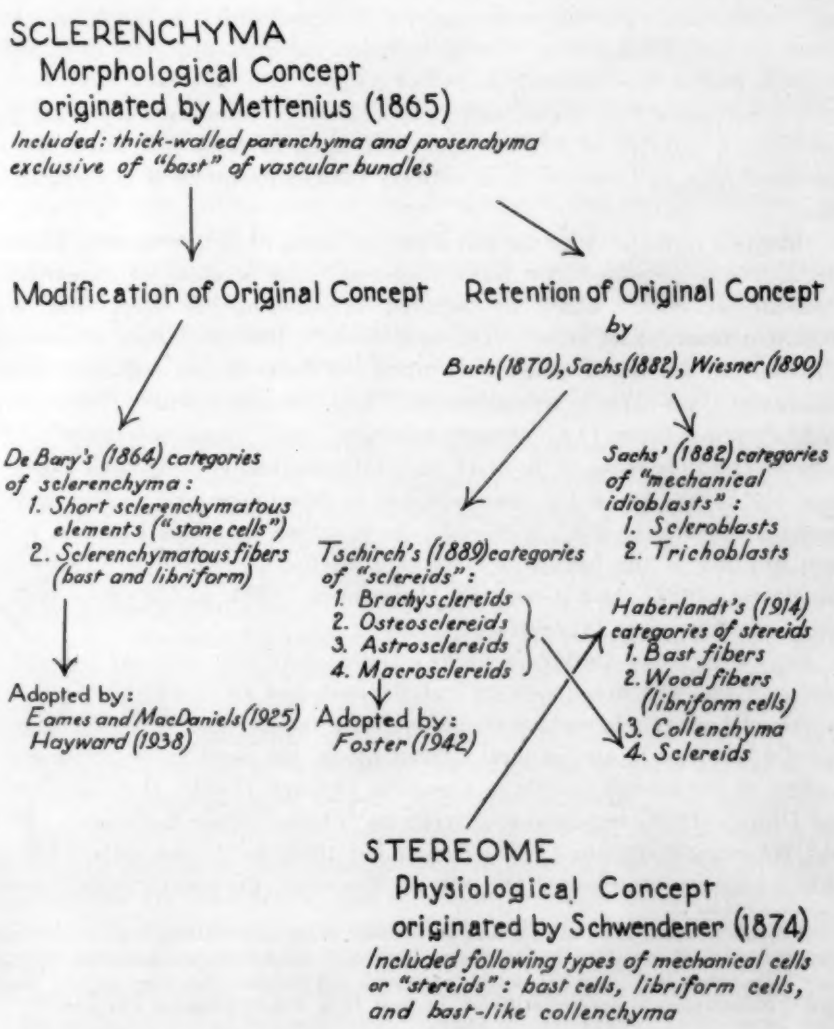
TABLE 1. *Summary of the terms which have been used in attempting to classify morphologically the branched cells in the leaf of Camellia.*
All authors in this table are listed under "Literature Cited."

Term	Originator	Applied to branched cells of *Camellia* leaf by
Fibers	?	Mirbel and Payen (1849, 1850); DeBary (1884); Dippel (1898)
Sclerenchyma cells	Mettenius (1865)	Mettenius (1865); Buch (1870); Wiesner (1890); Palladin (1911)
Bast cells	?	Hofmeister (1867)
Idioblasts	Sachs (1874)	Cavara (1897); Kochs (1900); Solereder (1908)
Trichoblasts	Sachs (1882)	Sachs (1882); Luerssen (1893)
Sclereids	Tschirch (1885)	Melchior (1925); Puchinger (1923)
Astrosclereids	Tschirch (1885)	Tschirch (1885, 1889); Haberlandt (1914); Jackson (1916); Küster (1935); Foster (1942)
Bast fibers	?	Goodale (1885)
Stone cells	?	Schumann (1889); Warming-Johansen (1909)
Stereocytes	Chodat (1920)	Chodat (1920)
Sclerites	Seward (1906)	Beauvisage (1920)

from an historical standpoint, it at once becomes clear that much of the confusion has arisen from (1) the gradual modification of Mettenius's (1865) concept of "sclerenchyma," and (2) the strong influence of Schwendener's (1874) physiological classification of "mechanical elements."

TABLE 2. *Diagram showing the main steps in the historical development of the concepts of "sclerenchyma" and "stereome."*

All authors in this table are listed under "Literature Cited."



As is shown in table 2, the concept of sclerenchyma as originally defined by Mettenius (1865) included thick-walled "parenchyma" and "prosenchyma" *exclusive* of the bast fibers of the vascular system. Buch (1870, p. 16) accepted this idea and emphasized that his concept of "sclerenchyma cells" included "all strongly thickened cells lying outside the vascular bundle, regardless of the ultimate form of the cell." Mettenius cited as an example of sclerenchyma cells the isolated thick-walled elements in the petiole of *Camellia*, and his viewpoint was later adopted by Buch (1870), Wiesner (1890), and Palladin (1914). Sachs (1882) likewise accepted Mettenius's concept of sclerenchyma and proposed the terms "scleroblast" and "trichoblast" for sclerenchymatous idioblasts which do not form a true tissue. Under "trichoblasts," Sachs included the branched cells in *Camellia* leaves as well as the "internal hairs" of *Nuphar* and *Monstera*. Reference to table 1 will show that Sachs' more general term "idioblast" has been preferred by a number of writers, although when used in this sense for the branched cells of *Camellia* it is entirely noncommittal in a morphological sense.

Strongly influenced by the physiological ideas of Schwendener, Tschirch (1885, 1889) proposed the term "sclereid" for a class of thick-walled "mechanical cells" which he believed are distinct in form and wall-structure from "bast cells" (i.e., bast fibers). His categories of sclereids (cf. table 2) are based principally upon the *form* of the cell and include idioblastic types (i.e., "osteosclereids" and "astrosclereids") as well as tissue-forming types (i.e., "brachysclereids" and "macrosclereids"). The term sclereid, because it is brief and etymologically clear, has much to commend it and hence has been adopted in this paper and in the writer's recent book (Foster 1942, p. 67–72). As is shown in tables 1 and 2, it has been applied to the branched cells of *Camellia* by Melchior (1925) and Puchinger (1923), and is used by Haberlandt (1914, p. 158) to designate one of the four main types of "stereids."[6]

Beginning with DeBary's (1884) classic text, the original concept of sclerenchyma was broadened to include bast and libriform fibers as well as "short" sclerenchymatous elements (e.g., "stone cells"). Unfortunately this did not lead to any general agreement on the most appropriate classification of the branched cells in *Camellia*. DeBary (1884), Goodale (1885), and Dippel (1898) regarded these cells as "fibers," while Schumann (1889) and Warming-Johansen (1909) designated them as "stone cells." Chodat (1920) likewise interpreted the cells as fibers and his special term "stereo-

[6] It will be noted from table 2 that Haberlandt recognizes collenchyma as a category coordinate with fibers and sclereids. Since "typical" collenchyma cells develop only primary walls (Esau 1936) and are capable of growth and division even when mature, Haberlandt's classification is open to criticism, at least from a morphological standpoint.

cytes'' reflects the additional influence of Schwendener (cf. table 2). The term ''sclerites'' is not obviously related either to the concept of ''sclerenchyma'' or ''stereome.'' It was applied by Seward (1906) to the branched idioblasts found in the leaves of *Araucaria* and *Agathis* and was employed in a similar way for the branched cells of *Camellia* by Beauvisage (1920) in his monograph on the *Ternstroemiaceae*.

From the historical analysis just given and in the light of the present investigation, it is evident that the whole concept of sclerenchyma merits careful re-examination. Solereder (1908, p. 1091–1092) lists 84 families of dicotyledons in which idioblastic ''sclerenchyma'' cells occur in the mesophyll of the leaf. He rather loosely terms all such elements ''spicular cells,'' apparently adopting the term from Hooker's (1864) designation of the remarkable crystal-bearing cells found in *Welwitchia*. According to Matsuda (1894, p. 128; pl. IV, fig. 20) crystal-bearing sclerenchyma cells, essentially similar to those of *Welwitchia*, occur in the dicotyledon *Kadsura japonica*. The need for broad comparative studies is thus very clear. They should include investigations not only on cell development but also on the structure and chemical make-up of the secondary wall. Important advances in this direction have already been made on fibers of various types by Bailey and Kerr (1935) and Esau (1938, 1943). When more data are available, it may be possible to differentiate more scientifically a series of categories under ''sclerenchyma.'' It seems clear that both fibers and sclereids of various types would occur in any morphological classification of this kind.

Postscript. After completing the entire manuscript for this paper, the writer ''discovered'' a much-neglected treatise on the comparative morphology and functions of sclereids in seed plants. This remarkable work, consisting of 96 pages of text and 3 plates, was written in 1890 by C. J. Wijnaendts Francken and appeared as a printed dissertation from Utrecht University under the title of ''De Sclereïden.'' The fact that this dissertation was not subsequently published in a scientific journal doubtless explains why it has not been more widely noted in histological literature. Apparently the only previous allusion to it is by Solereder (1908), who includes it among the literature ''references'' under certain dicotyledonous families. With the indispensable aid in translation given by the writer's colleague, Dr. George F. Papenfuss, it is evident that ''De Sclereïden'' is monographic in scope. It includes not only a description of sclereid morphology in seed plants (14 genera of gymnosperms and representatives of 14 families of angiosperms are considered) but it also attempts to review critically the problems of terminology and classification of the varied forms of idioblastic sclereids from much the same standpoint which has been adopted by the present writer. Wijnaendts Francken was evidently strongly influenced by the ideas of Schwendener, Tschirch, and Haberlandt, as is shown

by his effort to demarcate sharply between "bast fibers" and "sclereids." While recognizing that intergradations occur between these two cell types, he concludes that sufficient differences exist to justify separate terms for them. He also emphasizes that although sclereids usually originate from "ground tissue" cells, their distribution within organs is so varied that they cannot be regarded as a "unity" either ontogenetically or phylogenetically. As regards the Ternstroemiaceae, he investigated the sclereids of *Camellia japonica*, *C. sasangua*, *Thea viridis*, and *T. Bohea*. In *Camellia* he was unable to detect, even by using reagents, any lamellae in the secondary wall and he described the latter as "homogeneous." This observation is supported by the present investigation. Space does not permit further discussion, but the writer desires to emphasize his belief that "De Sclereïden" deserves the attention of modern workers and should serve as a valuable orientation for the much-needed comparative investigations on sclereids in seed plants.

SUMMARY

This paper describes a study of the structure and development of the sclereids in the petiole of *Camellia japonica*.

The sclereids occur as typical idioblasts distributed in the parenchyma of "cortex" and "pith." When isolated by maceration, the adult sclereids are remarkably polymorphic cells, ranging in shape from fusiform types to elaborately ramified elements. In all form-types, more or less numerous, short, conical or irregular protuberances are characteristic. These protuberances are termed "spicules" and their occurrence on the petiolar sclereids of *C. reticulata* and *C. sinensis* is noted.

Sclereids originate from parenchymatous cells of the cortex and pith of the petiole during the final phase of enlargement of the foliage leaf. The initial cells, despite their idioblastic distribution, can be identified by their greatly enlarged nuclei. During the earliest stages of development, the sclereid initial produces one or more delicate tubular branches which extend between the walls of neighboring tissue-elements and may ultimately penetrate certain of the intercellular air-spaces. The continued ramification of the sclereid is accompanied by the origin and development of "spicules" which, like the major branches, grow in between the walls of adjacent parenchyma cells. Throughout the life of the sclereid, the protoplast remains uninucleate.

When the sclereid has completed its intercellular development, a massive secondary wall, traversed by slender and often ramiform pit-canals, is produced. A pit-canal consists of a cone-shaped channel extending from the lumen to the small circular chamber. The latter is slightly overarched by the secondary wall and is paired with a pit-field in the wall of the adjacent parenchyma cell.

The intercellular development of the sclereid is discussed with reference to the theories of "gliding" and "intrusive" growth. While the latter type of growth probably occurs during spicule development, the elongation of the major branches is not necessarily restricted to their tips.

The problem of classifying the sclereids of *Camellia* morphologically is discussed and the confused terminology is examined in the light of the historical development of the concepts of "sclerenchyma" and "stereome." The need for comparative studies on the development and wall structure of sclerenchymatous cells is emphasized.

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Literature Cited

Bailey, I. W. 1923. The cambium and its derivative tissues. IV. The increase in girth of the cambium. Am. Jour. Bot. **10**: 499–509.

Bailey, I. W. & Faull, A. F. 1934. The cambium and its derivative tissues. IX. Structural variability in the redwood, *Sequoia sempervirens*, and its significance in the identification of fossil woods. Jour. Arnold Arb. **15**: 233–254.

Bailey, I. W. & Kerr, T. 1935. The visible structure of the secondary wall and its significance in physical and chemical investigations of tracheary cells and fibers. Jour. Arnold Arb. **16**: 273–300.

Ball, E. 1941. Microtechnique for the shoot apex. Am. Jour. Bot. **28**: 233–243.

Beauvisage, L. 1920. Contribution à l'étude anatomique de la famille des Ternstroemiaceae. Thèse, Fac. Sci. Poitiers.

Buch, O. 1870. Ueber Sklerenchymzellen. Diss. Breslau.

Cavara, F. 1897. Contributo alla morfologia ed allo sviluppo degli idioblasti delle Camelliee. Atti Inst. Bot. Univ. Pavia **4**: 61–87.

Chodat, R. 1920. Principes de botanique. ed. 3.

DeBary, A. 1884. Comparative anatomy of the vegetative organs of the phanerogams and ferns.

Dippel, L. 1898. Das Mikroskop und seine Anwendung. Zweiten Teil. Anwendung des Mikroskopes auf die Histologie der Gewächse. ed. 2.

Eames, A. J. & MacDaniels, L. H. 1925. An introduction to plant anatomy.

Esau, K. 1936. Ontogeny and structure of collenchyma and of vascular tissues in celery petioles. Hilgardia **10**: 431–467.

———. 1938. The multinucleate condition in fibers of tobacco. Hilgardia **11**: 427–434.

———. 1943. Vascular differentiation in the vegetative shoot of *Linum*. III. The origin of the bast fibers. Am. Jour. Bot. **30**: 579–586.

Foster, A. S. 1934. The use of tannic acid and iron chloride for staining cell walls in meristematic tissue. Stain Tech. **9**: 91–92.

———. 1942. Practical plant anatomy.

Goodale, G. L. 1885. Gray's botanical textbook. ed. 6. Vol II. Physiological botany.

Haberlandt, G. 1914. Physiological plant anatomy.

Hayward, H. E. 1938. The structure of economic plants.

Hofmeister, W. 1867. Handbuch d. physiologischen Botanik. Bd. 1. Die Lehre von der Pflanzenzelle.

Hooker, J. D. 1864. On *Welwitchia*, a new genus of the Gnetaceae. Trans. Linn. Soc. **24**: 1–48.

Jackson, B. D. 1916. A glossary of botanic terms. ed. 3.

Kerr, T. & Bailey, I. W. 1934. The cambium and its derivative tissues. X. Structure, optical properties and chemical composition of the so-called middle lamella. Jour. Arnold Arb. **15**: 327–349.

Kochs, J. 1900. Über die Gattung *Thea* und den chinensischen Thee. Bot. Jahrb. **27**: 577–635.

Küster, E. 1935. Die Pflanzenzelle.

Luerssen, C. 1893. Grundzüge der Botanik.

Majumdar, G. P. 1941. The sliding, gliding, symplastic or the intrusive growth of the cambium cells and their derivatives in higher plants. Jour. Indian Bot. Soc. **20**: 161–171.

Matsuda, S. 1894. On the anatomy of Magnoliaceae. Coll. Sci. Univ. Jap. Jour. **6**: 115–149.

Melchior, H. 1925. Theaceae. *In:* Engler, A. & Prantl, K. Die naturlichen Pflanzenfamilien. ed. 2. **21**: 109–154.

Mettenius, G. 1865. Über die Hymenophyllaceae. Abhand. Sächs. Gesell. Wiss. Math.-Phys. **7**: 403–504.

Mirbel, C. F. & Payen, A. 1849. Organographie et physiologie vegetale. Mémoire sur la composition et la structure de plusieurs organismes des plantes. Mém. Acad. Sci. Inst. France **20**: 497–531.

———— & ————. 1850. [Same title as above. Contains explanation of plates I–XVI, together with all except plates I and III which appear above with text.] Mém. Acad. Sci. Inst. France **22**: 525–568.

Palladin, W. I. 1914. Pflanzenanatomie. Trans. from 5th Russian ed.

Paton, J. B. 1921. Pollen and pollen enzymes. Am. Jour. Bot. **8**: 471–501.

Priestley, J. H. 1930. Studies in the physiology of cambial activity. II. The concept of sliding growth. New Phytol. **29**: 96–140.

Priestley, J. H. & Scott, L. I. 1938. An introduction to botany.

Puchinger, H. 1923. Über die Lebensdauer sclerotisierter Zellen. Sitzungsber. Akad. Wiss. Wien. Math.-Naturwiss. I. **131**: 47–57.

Sachs, J. 1882. Text-book of botany.

Sass, J. E. 1940. Elements of botanical microtechnique.

Schumann, C. R. G. 1889. Anatomische Studien über die Knospenschuppen von Coniferen und dicotylen Holzgewächsen. Biblioth. Bot. **3**(15): 1–32.

Schwendener, S. 1874. Das mechanische Princip im anatomischen Bau der Monocotylen.

Seward, A. C. 1906. The Araucarieae, recent and extinct. Phil. Trans. Roy. Soc. B. **198**: 305–411.

Sinnott, E. W. & Bloch, R. 1939. Changes in intercellular relationships during the growth and differentiation of living plant tissues. Am. Jour. Bot. **26**: 625–634.

———— & ————. 1943. Development of the fibrous net in the fruit of various races of *Luffa cylindrica*. Bot. Gaz. **105**: 90–99.

Solereder, H. 1908. Systematic anatomy of the dicotyledons. Vol. II.

Thomas, F. 1865. Zur vergleichenden Anatomie der Coniferen-Laubblätter. Jahrb. Wiss. Bot. **4**: 23–63.

Tschirch, A. 1885. Beiträge zur Kenntniss des mechanischen Gewebesystems der Pflanzen. Jahrb. Wiss. Bot. **16**: 303–335.

————. 1889. Angewandte Pflanzenanatomie.

Vöchting, H. 1908. Untersuchungen zur experimentellen Anatomie und Pathologie der Pflanzenkörpers.

Warming-Johansen. 1909. Lehrbuch der allgemeinen Botanik.

Wiesner, J. 1890. Anatomie und Physiologie der Pflanzen.

INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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PLANT TAXONOMY AND FLORISTICS

(exclusive of fungi)

(See also under Genetics: **Babcock & Jenkins**)

Alexander, E. J. *Clematis heracleifolia Davidiana.* Father David's Clematis. Native of north and central China. Addisonia **22**: 11, 12. *pl. 710.* Ap 1943 [3 Mr 1944].

Alexander, E. J. *Eryngium synchaetum.* Native of southeastern United States. Addisonia **22**: 13, 14. *pl. 711.* Ap 1943 [3 Mr 1944].

Alexander, E. J. *Sedum stenopetalum.* Native of western North America. Addisonia **22**: 5, 6. *pl. 707.* Ap 1943 [3 Mr 1944].

Allen, C. K. *Nectandra coriacea.* Sweetwood. Native of Florida, Yucatan and the West Indies. Addisonia **22**: 9, 10, 12. *pl. 709.* Ap 1943 [3 Mr 1944].

Alvarado Montesdeoca, V. Una excursión botánica al Chimborazo. Bol. Inst. Bot. [Quito] $2^{3,4}$: 18–36. *f. 1–5.* 5 O 1943.

Andrews, L. R. Taxonomic notes. III. Further synonyms of *Hymenostylium curvirostrum.* Bryologist **46**: 131–135. D 1943 [20 Ja 1944].

Babcock, E. B. & Stebbins, G. L. Systematic studies in the Cichorieae. Univ. Cal. Publ. Bot. **18**: 227–240. *f. 1–6.* 2 N 1943.

Bailey, L. H. Species Batorum. The genus *Rubus* in North America (north of Mexico). VII. Section 8. Canadenses. Gentes Herb. **5**: 465–503. *pl. 211–228.* 16 F 1944.

Barkley, F. A. Noteworthy plants of Texas. II. A new species of *Peltandra.* Madroño **7**: 131–133. *pl. 21.* Ja [2 F] 1944.

Barneby, R. C. A note on the distribution of some western Dicotyledons. Leafl. West. Bot. **4**: 7–12. 2 F 1944.

Beetle, A. A. A new name in *Scirpus.* Madroño **7**: 160. Ja [2 F] 1944.

Beetle, D. E. A monograph of the North American species of *Fritillaria.* Madroño **7**: 133–159. *f. 1–4.* Ja [2 F] 1944.

Boyle, W. S. Cytological evidence for the taxonomic position of *Schizachne purpurascens.* Madroño **7**: 129, 130. *f. 1.* J [2 F] 1944.

Butters, F. K. The American variety of *Saxifraga Aizoon.* Rhodora **46**: 61–69. *pl. 817.* Mr 1944.

Camp, W. H. Another new name in *Vaccinium.* Bull. Torrey Club **71**: 179, 180. 1 Mr 1944.

Clausen, R. T. A description and name for *Sedum X Y Z.* Cactus & Succ. Jour. **16**: 7, 8. *f. 5, 6.* Ja 1944.

Conzatti, C. Flora taxonomica mexicana. **2**: 1–279. Monocotiledoneas. Ap 1941 [Ja 1944].

Correll, D. S. Orchidaceae. *In:* Flora of Texas **3**^{a}: 151–196. *pl. 1–34.* Southern Methodist Univ. [Mr] 1944.

Croizat, L. New Euphorbiaceae from the Island of Mauritius. Trop. Woods **77**: 13–18. 1 Mr 1944.

Croizat, L. A study of the genus *Lophophora* Coulter II. Desert **15**: 152–154. D 1943 [F 1944]. III. **16**: 7–9. Ja [Mr] 1944.

D[aniel], H. Plantas colleccionadas en una excursión al Salto de Guadalupe. Bol. Inst. Bot. [Quito] **2**^{3,4}: 126–128. 5 O 1943.

Daniel, H. Una ascensión al Cerro de "La Vieja." Bol. Inst. Bot. [Quito] **2**^{3,4}: 120–126. 5 O 1943.

Dixon, H. N. Notes on *Fissidens japonicus.* Bryologist **46**: 128–131. D 1943 [20 Ja 1944].

Duncan, W. H. A new species of *Baptisia.* Rhodora **46**: 29–31. *f. 1–5.* 12 F 1944.

Dwyer, J. D. A discussion of the ochnaceous genus *Fleurydora* A. Chev. and the allied genera of the Luxemburgieae. Bull. Torrey Club **71**: 175–178. *f. 1.* 1 Mr 1944.

Eastwood, A. A new manzanita from Baja California. Leafl. West. Bot. **4**: 4, 5. 2 F 1944.

Fernald, M. L. A further item on *Lilium michiganense.* Rhodora **46**: 86, 87. Mr 1944.

Fernald, M. L. Overlooked species, transfers and novelties in the flora of eastern North America. Rhodora **46**: 1–21. *pl. 807–811.* 22 Ja 1944. 32–57. *pl. 812–816.* 12 F 1944.

Fernald, M. L. *Setaria Faberii* in eastern America. Rhodora **46**: 57, 58. 12 F 1944.

Fernald, M. L. The so-called keeled garlic of eastern Pennsylvania. Rhodora **46**: 59, 60. 12 F 1944.

Fernald, M. L. *Spergula pentandra* in America. Rhodora **46**: 88. Mr 1944.

Fox, H. M. Lavandula abrotanoides. Canary lavender. Native of the Canary Islands. Addisonia **22**: 7, 8. *pl. 708.* Ap 1943 [3 Mr 1944].

Frye, T. C. & Ferguson, E. *Pogonatum liebmannianum.* Bryologist **46**: 141–146. *f. 1–25.* D 1943 [20 Ja 1944].

Hodgdon, A. R. *Lilium superbum* and other isolated species in Durham, New Hampshire. Rhodora **46**: 21–23. 22 Ja 1944.

Hoover, R. F. *Mariposa,* a neglected genus. Leafl. West. Bot. **4**: 1–4. 2 F 1944.

Hopkins, M. *Cercis,* its taxonomic relationship in the Oklahoma flora. Proc. Okla. Acad. **22**: 130, 131. 1942.

Hopkins, M. New plants for the Oklahoma flora. Proc. Okla. Acad. **23**: 29, 30. 1943.

Howell, J. T. A new fruticulose *Eriogonum.* Leafl. Wes'. Bot. **4**: 5–7. 2 F 1944.

Howell, J. T. A reconsideration of the genus *Miltitzia.* Leafl. West. Bot. **4**: 12–16. 2 F 1944.

Howell, J. T. Two Lake County records. Leafl. West. Bot. **4**: 16. 2 F 1944.

Hunziker, A. T. Las especies alimenticias de *Amaranthus* y *Chenopodium* cultivadas por los Indios de América. Rev. Arg. Agron. **10**: 297–354. *pl. 21–28. f. 1–15.* 5 D 1943.

Jones, G. N. *Geranium nervosum.* Rhodora **46**: 28. 22 Ja 1944.

Lakela, O. Notes on Minnesota plant life. Rhodora **46**: 25–28. 22 Ja 1944.

Little, E. L. American smoketree (*Cotinus obovatus* Raf.), one of Oklahoma's rarest tree species. Proc. Okla. Acad. **23**: 21–23. 1943.

Little, E. L. Later generic homonyms among North American mosses. Bryologist **46**: 105–125. D 1943 [20 Ja 1944].

Lowe, C. W. List of flowering plants, ferns, club mosses, mosses and liverworts of Manitoba. 1–110. Nat. Hist. Soc. Manitoba. N 1943.

Marie-Victorin, *Frère*. Les hautes pinèdes d'Haiti. Nat. Canad. **70**: 245–258. *f. 1–12*. N–D 1943 [14 F 1944].

Maxon, W. R. *Diplazium lonchophyllum* in Louisiana. Am. Fern Jour. **34**: 21–24. J–Mr 1944.

Maxon, W. R. *Nephrolepis tuberosa* (Willd.) Presl. Am. Fern Jour. **34**: 25. Ja–Mr 1944.

Maxon, W. R. Three new species of *Alsophila* from Colombia and British Honduras. Jour. Wash. Acad. **34**: 46–49. *f. 1*. 15 F 1944.

Mille, P. L. El algarrobo. Bol. Inst. Bot. [Quito] $2^{3,4}$: 159–162. 5 O 1943.

Monachino, J. A Colombian species of *Sterigmapetalum*. Trop. Woods 77: 10–12. 1 Mr 1944.

Monachino, J. *Herniaria glabra*, var. *subciliata* in New York. Rhodora **46**: 23–25. 22 Ja 1944.

Monachino, J. A revision of *Couma* and *Parahancornia* (Apocynaceae). Lloydia 6: 229–247. D 1943 [F 1944].

Moraes Mello, E. M. & Sampaio Fernandes, J. Contribuicão ao estudo das plantas toxicas Brasileiras. Rio de Janeiro—Ministerio da Agric. 1–106p. *6 col. pl. + f. 1–3*. 1941.

Morton, C. V. A new *Trichomanes* from Colombia. Am. Fern Jour. **34**: 19, 20. *1 f.* Ja–Mr 1944.

Munz, P. A. Studies in Onagraceae—XIII. The American species of *Ludwigia*. Bull. Torrey Club **71**: 152–165. 1 Mr 1944.

Papenfuss, G. F. Notes on algal nomenclature. III. Miscellaneous species of Chlorophyceae, Phaeophyceae, and Rhodophyceae. Farlowia **1**: 337–346. Ja 1944.

Parodi, L. R. Una nueva especie de "*Sorghum*" cultivada en la Argentina. Rev. Arg. Agron. **10**: 361–372. *pl. 31–34 + f. 1–3*. 5 D 1943.

Patterson, P. M. Additional mosses from Mountain Lake, Virginia. Bryologist 46: 126–128. D 1943 [20 Ja 1944].

Pease, A. S. *Cirsium Flodmani* in New England. Rhodora **46**: 87, 88. Mr 1944.

Prescott, G. W. New species and varieties of Wisconsin algae. Farlowia **1**: 347–385. *pl. 1–5 + f. 1*. Ja 1944.

Raymond, M. Quelques progrès récents dans la connaissance des *Carex* du Québec. Nat. Canad. **70**: 259–278. *f. 1, 2*. N–D 1943 [14 F 1944].

Record, S. J. Random observations on Tropical-American timbers. Trop. Woods 77: 1–10. 1 Mr 1944.

Rousseau, J. Deux nouveaux *Astragalus* du Québec. Nat. Canad. **71**: 5–14. *f. 1, 2*. Ja–F [Mr] 1944.

Schweinfurth, C. Notes on Peruvian orchids. Bot. Mus. Leafl. **11**: 215, 216. Mr 1944.

Schweinfurth, C. Notes on tropical American orchids. Bot. Mus. Leafl. **11**: 173–200. 7 F 1944.

Schweinfurth, C. A novelty in *Xylobium* from Peru. Am. Orchid Soc. Bull. **12**: 350–352. *1 pl.* 1 Mr 1944.

Sebold, H. R. *Lonicera Standishii.* Native of China. Addisonia **22**: 15, 16. *pl. 712.* Ap 1943 [3 Mr 1944].

Shinners, L. H. *Aster acadiensis* nom. nov. Rhodora **46**: 31. 12 F 1944.

Smith, A. C. Reminiscences of fern collecting in Fiji. Am. Fern Jour. **34**: 1–16. *pl. 1, 2.* Ja–Mr 1944.

Smith, C. P. Species *Lupinorum.* Saratoga, Cal. 305–320. 7 Ja 1942. 321–326. D 1943. 337–368. Ja 1944. 369–384. F 1944. 385–400. F 1944.

Smith, Mrs. F. C. A fern new to Worcester County, Massachusetts. Am. Fern Jour. **34**: 24. Ja–Mr 1944.

Standley, P. C. & Steyermark, J. A. Studies of Central American plants—IV. Field Mus. Bot. Ser. **23**: 31–109. 14 F 1944. V. 113–150. 24 Mr 1944.

Stewart, R. R. *Polygonatum oppositifolium.* Native of central and eastern Himalaya. Addisonia **22**: 3, 4. *pl. 706.* Ap 1943 [3 Mr 1944].

Summerhayes, V. S. African orchids. XIV. Bot. Mus. Leafl. 11: 201–214. 3 Mr 1944.

Tansey, J. W. *Hexisea bidentata.* Native of Central America. Addisonia **22**: 1, 2. *pl. 705.* Ap 1943 [3 Mr 1944].

Tiffany, L. H. & Britton, M. E. Freshwater Chlorophyceae and Xanthophyceae from Puerto Rico. Ohio Jour. Sci. **45**: 39–50. Ja 1944.

Vargas C., C. Nuevas especies de papas silvestres del Perú. Rev. Arg. Agron. **10**: 396–398. 5 D 1943.

Weatherby, C. A. A southern variety of *Polypodium peltatum.* Am. Fern Jour. **34**: 17–19. Ja–Mr 1944.

Wherry, E. T. Note on the southeastern relatives of *Lycopodium inundatum.* Am. Fern Jour. **34**: 24. Ja–Mr 1944.

Wynne, F. E. *Drosera* in eastern North America. Bull. Torrey Club **71**: 166–174. *f. 1–12.* 1 Mr 1944.

Wynne, F. E. Range extensions of mosses in western North America. Bryologist **46**: 149–155. *f. 1, 2.* D 1943 [20 Ja 1944].

MORPHOLOGY

(including anatomy, and cytology in part)
(See also under Plant Physiology: **Riley**)

Blaser, H. W. Studies in the morphology of the Cyperaceae. II. The prophyll. Am. Jour. Bot. **31**: 53–64. *f. 1–55.* Ja [7 F] 1944.

Bloch, R. Developmental potency, differentiation and pattern in meristems of *Monstera deliciosa.* Am. Jour. Bot. **31**: 71–77. *f. 1–11.* F [Mr] 1944.

Cheadle, V. I. Specialization of vessels within the xylem of each organ in the Monocotyledoneae. Am. Jour. Bot. **31**: 81–92. *f. 1–11.* F [Mr] 1944.

Dodd, J. D. Three-dimensional cell shape in the carpel vesicles of *Citrus grandis.* Am. Jour. Bot. **31**: 120–127. *f. 1–19.* F [Mr] 1944.

Eigsti, O. J. The occurrence of a pollen tube with four sperms and two tube nuclei in *Polygonatum.* Proc. Okla. Acad. **22**: 134–136. *f. 1–5.* 1942.

Haupt, A. W. Multiple eggs in *Symphyogyna.* Bryologist **46**: 139–141. D 1943 [20 Ja 1944].

O'Donnell, C. A. & Rodriguez, J. M. Contribucion al conocimiento histologico de la materia medica indigena. Arch. Farm. Bioquim. **1**: 17–34. *pl. 1–3 + f. 1–8.* 1943.

Plymale, E. L. & Wylie, R. B. The major veins of mesomorphic leaves. Am. Jour. Bot. **31**: 99–106. *f. 1–9.* F [Mr] 1944.

Rimbach, A. El ajo silvestre (*Nothoscordum inodorum*). Bol. Inst. Bot. [Quito] $2^{3,4}$: 74–85. *f. 1–5.* 5 O 1943.

Skoog, F. Growth and organ formation in tobacco tissue cultures. Am. Jour. Bot. **31**: 19–24. *f. 1–6.* Ja [7 F] 1944.

Smith, G. M. Microaplanospores of *Vaucheria*. Farlowia **1**: 387–389. *f. 1, 2.* Ja 1944.

Steil, W. N. Peculiar fern prothalia. Bull. Torrey Club **71**: 93–98. *f. 1–9.* 25 Ja 1944.

Went, F. W. Morphological observations on the tomato plant. Bull. Torrey Club **71**: 77–92. *f. 1–22.* 25 Ja 1944.

PLANT PHYSIOLOGY

(See also under Morphology: **Skoog**; under Mycology: **Gottlieb, Waksman** *et al.*)

Allard, H. A. Length-of-day behavior of *Nicotiana gossei*. Jour. Agr. Res. **67**: 459–464. *f. 1–3.* 1943.

Bailey, L. F. & McHargue, J. S. Effect of boron, copper, manganese, and zinc in the enzyme activity of tomato and alfalfa plants grown in the greenhouse. Plant Physiol. **19**: 105–116. *f. 1–5.* Ja [Mr] 1944.

Berger, J. & Avery, G. S. Glutamic acid and isocitric acid dehydrogenases in the *Avena* coleoptile and the effect of auxins of these enzymes. Am. Jour. Bot. **31**: 11–19. *f. 1–8.* Ja [7 F] 1944.

Biddulph, O. & Markle, J. Translocation of radio-phosphorus in the phloem of the cotton plant. Am. Jour. Bot. **31**: 65–70. *f. 1–3.* F [Mr] 1944.

Brewer, G. E. F. & Godar, E. Buffer values of the leaves of some plants. Plant Physiol. **19**: 164–169. *f. 1, 2.* Ja [Mr] 1944.

Crafts, A. S. & Lorenz, O. A. Fruit growth and food transport in Cucurbits. Plant Physiol. **19**: 131–138. Ja [Mr] 1944.

Curtis, L. C. The exudation of glutamine from lawn grass. Plant Physiol. **19**: 1–5. *f. 1, 2.* Ja [Mr] 1944.

Emerson, R. L., Stauffer, J. F. & Umbreit, W. W. Relationships between phosphorylation and photosynthesis in *Chlorella*. Am. Jour. Bot. **31**: 107–120. *f. 1–3.* F [Mr] 1944.

Hoagland, D. R. Lectures on the inorganic nutrition of plants. 1–226p. *pl. 1–28.* Waltham, Chronica Botanica Co. 1944.

Johnstone, G. R. & Feeney, F. L. Periodicity of *Gelidium cartilagineum*, a perennial red alga. Am. Jour. Bot. **31**: 25–29. *f. 1–3.* Ja [7 F] 1944.

Pratt, R. Influence of light on the infection of wheat by the powdery mildew, *Erysiphe graminis tritici*. Bull. Torrey Club **71**: 134–143. *f. 1, 2. t. 1–3.* 1 Mr 1944.

Riley, H. P. Relative growth of flower parts of two species of *Iris*. Bull. Torrey Club **71**: 122–133. *f. 1–8, t. 1.* 1 Mr 1944.

Robbins, W. J. Plants need vitamins too. Torreya **43**: 116–125. D 1943 [10 F 1944].

Robbins, W. J. & Kavanagh, F. Temperature, thiamine, and growth of *Phycomyces*. Bull. Torrey Club **71**: 1–10. *f. 1–3, t. 1–3.* 25 Ja 1944.

Sideris, C. P. & Young, H. Y. Effects of iron on chlorophyllous pigments, ascorbic acid, acidity and carbohydrates of *Ananas comosus* (L.) Merr., supplied with nitrate or ammonium salts. Plant Physiol. **19**: 52–75. *f. 1–16.* Ja [Mr] 1944.

Sweeney, B. M. The effect of auxin on protoplasmic streaming in root hairs of *Avena*. Am. Jour. Bot. **31**: 78–80. *f. 1–3.* F [Mr] 1944.

Taylor, H. A physiological study of diploid and related tetrapolid plants. Proc. Okla. Acad. **22**: 137, 138. 1942.

Thut, H. F. & Loomis, W. E. Relation of light to growth of plants. Plant Physiol. **19**: 117–130. *f. 1–8.* Ja [Mr] 1944.

Tingley, M. A. Concentration gradients in plant exudates with reference to the mechanism of translocation. Am. Jour. Bot. **31**: 30–38. Ja [7 F] 1944.

Vlamis, J. & Davis, A. R. Effects of oxygen tension on certain physiological responses of rice, barley and tomato. Plant Physiol. **19**: 33–51. *f. 1–9.* Ja [Mr] 1944.

Zimmerman, P. W. The formative influences and comparative effectiveness of various plant hormone-like compounds. Torreya **43**: 98–115. *f. 1–4, t. 1–5.* D 1943 [10 F 1944].

GENETICS
(including cytogenetics)
(See also under Taxonomy: **Boyle**; under Plant Physiology: **Taylor**)

Babcock, E. B. & Jenkins, J. A. Chromosomes and phylogeny of *Crepis*. III. The relationships of one hundred and thirteen species. Univ. Cal. Publ. Bot. **18**: 241–291. *f. 1–24.* 30 N 1943.

Cave, M. S. & Constance, L. Chromosome numbers in the Hydrophyllaceae: II. Univ. Cal. Publ. Bot. **18**: 293–298. *f. 1–3.* 29 Ja 1944.

Eigsti, O. J. & Taylor, H. The induction of polyploidy in *Phlox* by colchicine. Proc. Okla. Acad. **22**: 120–122. *1 pl.* 1942.

Myers, W. M. The randomness of chromosome distribution at anaphase I in autotriploid *Lolium perenne* L. Bull. Torrey Club **71**: 144–151. *f. 1–5, t. 1–3.* 1 Mr 1944.

Rife, D. C. The genetics of certain common variations in *Coleus*. Ohio Jour. Sci. **45**: 18–24. *f. 1.* Ja 1944.

Rollins, R. C. Evidence for natural hybridity between Guayule (*Parthenium argentatum*) and Mariola (*Parthenium incanum*). Am. Jour. Bot. **31**: 93–99. *f. 1–10.* F [Mr] 1944.

Shull, G. H. Genetics, the unifying sicence in biology. Torreya **43**: 126–131. D 1943 [10 F 1944].

Stebbins, G. L. & Tobgy, H. A. The cytogenetics of hybrids in *Bromus*. I. Hybrids within the section *Ceratochloa*. Am. Jour. Bot. **31**: 1–11. *f. 1–16.* Ja [7 F] 1944.

MYCOLOGY
(See also under Plant Physiology: **Pratt**)

Barghoorn, E. S. & Linder, D. H. Marine fungi: Their taxonomy and biology. Farlowia **1**: 395–467. *pl. 1–7.* + *f. 1–3.* Ja 1944.

Bennett, C. W. Latent virus of dodder and its effect on sugar beet and other plants. Phytopathology **34**: 77–91. *f. 1–7.* Ja 1944.

Berkeley, G. H. Root-rots of certain non-cereal crops. Bot. Rev. **10**: 67–123. F 1944.

Burlingham, G. S. Studies in North American Russulae. Mycologia **36**: 104–120. *f. 1–2.* Ja–F 1944.

Carvajal, F. & Edgerton, C. W. The perfect stage of *Colletotrichum falcatum*. Phytopathology **34**: 206–213. *f. 1–5.* F 1944.

Chester, K. S. Physiogenic brooming in Chinese elm. Proc. Okla. Acad. **23**: 46–49. *f. 1.* 1943.

Costa, A. S. Multiplication of viruses in the dodder, *Cuscuta campestris*. Phytopathology **34**: 151–162. *f. 1.* F 1944.

Davidson, R. W. & Campbell, W. A. Observations on a gall of sugar maple. Phytopathology **34**: 132–135. *f. 1, 2.* Ja 1944.

Fitzpatrick, H. M. The first twelve years of the Mycological Society of America. Mycologia **36**: 1–17. *port.* Ja–F 1944.

Gottlieb, D. The mechanism of wilting caused by *Fusarium bulbigenum* var. *lycopersici*. Phytopathology **34**: 41–59. *f. 1, 2.* Ja 1944.

Hansen, H. N. & Rawlins, T. E. *Cercospora* fruit and leaf spot of olive. Phytopathology **34**: 257–259. *f. 1.* F 1944.

Hardison, J. R. Specialization of pathogenicity in *Erysiphe graminis* on wild and cultivated grasses. Phytopathology **34**: 1–20. Ja 1944.

Herre, A. W. C. T. A neglected field of study with the description of a new lichen from California. Farlowia **1**: 391–393. Ja 1944.

Hildebrand, E. N. New strain of *Agrobacterium rubi* from Boysenberry. Phytopathology **34**: 259, 260. *f. 1.* F 1944.

Humphrey, H. B. & Dufrenoy, J. Host-parasite relationship between the oat plant (*Avena* spp.) and crown rust (*Puccinia coronata*). Phytopathology **34**: 21–40. *f. 1–6.* Ja 1944.

Jauch, C. La presencia de "*Cylindrocladium scoparium*" en la Argentina. Rev. Arg. Agron. **10**: 355–360. *pl. 29, 30. f. 1, 2.* 5 D 1943.

Karling, J. S. *Phagomyxa algarum* n. gen., n. sp., an unusual parasite with plasmodiophoralean and proteomyxean characteristics. Am. Jour. Bot. **31**: 38–52. *f. 1–74.* Ja [7 F] 1944.

Kern, F. D. & Thurston, H. W. Additions to the Uredinales of Venezuela—III. Mycologia **36**: 54–64. Ja–F 1944.

Kunkel, L. O. Viruses in relation to the growth of plants. Torreya **40**: 87–95. *f. 1–9.* D 1943 [10 F 1944].

Lepage, E. Les lichens, les mousses et les hépatiques du Québec. II. Nat. Canad. **70**: 282–289. N–D 1943 [F 1944.] III. Deuxième section. Étude sommaire de la Pédologie. **71**: 40–46. Ja–F [Mr] 1944.

McClellan, W. D. A seedling blight of castor bean, *Ricinus communis*. Phytopathology **34**: 223–229. *f. 1–4.* F 1944.

McCubbin, W. A. Relation of spore dimensions to their rate of fall. Phytopathology **34**: 230–234. F 1944.

McKinney, H. H. & Clayton, E. E. Acute and chronic symptoms in the tobacco ring-spot disease. Phytopatholgy **34**: 60–76. *f 1–4.* Ja 1944.

Mundkur, B. B. *Tilletia tumefaciens*, a remarkable gall-forming smut from India. Phytopathology **34**: 143–146. *f. 1–4.* Ja 1944.

Negroni, P. Sobre el *Paecilomyces Burci* (Pollacci) Thom., como probable hongo entomógeno de la mariposa. Rev. Inst. Bact. [Buenos Aires] **11**: 265–267. *pl. 24, 25.* 8 N 1943.

Newhall, A. G. A serious storage rot of celery caused by the fungus *Ansatospora macrospora* n. gen. Phytopathology **34**: 92–105. *f. 1–3.* Ja 1944.

Nickerson, W. J. Studies in the genus *Zygosaccharomyces* I. Transfer of Pellicle-forming yeasts to *Zygopichia*. Farlowia **1**: 469–481. Ja 1944.

Orton, C. R. Graminicolous species of *Phyllachora* in North America. Mycologia **36**: 18–53. Ja–F 1944.

Reed, G. M. Phytopathology—1867–1942. Torreya **43**: 155–169. D 1943 [10 F 1944].

Rogers, D. P. The genera *Trechispora* and *Galzinia* (Thelephoraceae). Mycologia **36**: 70–103. *f. 1–14.* Ja–F 1944.

Singer, R. Notes on taxonomy and nomenclature of the polypores. Mycologia **36**: 65–69. Ja–F 1944.

Sipe, F. P. Lichens of Crater Lake National Park. Bryologist **46**: 135–138. D 1943 [20 Ja 1944].

Smith, A. H. & Hesler, L. R. New and interesting *Agarics* from Tennessee and North Carolina. Lloydia **6**: 248–266. *pl.1–4, f. 1.* D 1943. [F 1944].

Sprague, R. *Phoma terrestris* on Gramineae in the northern Great Plains. Phytopathology **34**: 129–131. Ja 1944.

Stevens, N. E. Cranberry false blossom in relation to flooding water. Phytopathology **34**: 140–142. Ja 1944.

Tervet, I. W. The relation of seed quality to the development of smut in oats. Phytopathology **34**: 105–115. Ja 1944.

Ullstrup, A. J. Further studies on a species of *Helminthosporium* parasitizing corn. Phytopathology **34**: 214–222. *f. 1–3.* F 1944.

Valleau, W. D., Johnson, E. M. & Diachun, S. Root infection of crop plants and weeds by tobacco leaf-spot bacteria. Phytopathology **34**: 163–174. *f. 1–3.* F 1944.

Waksman, S. A., Bugie, E. & Reilly, H. C. Bacteriostatic and bactericidal properties of antibiotic substances, with special reference to plant-pathogenic bacteria. Bull. Torrey Club **71**: 107–121. *t. 1–5.* 1 Mr 1944.

Wallace, J. M. & Lesley, J. W. Recovery from curly top in the tomato in relation to strains of the virus. Phytopathology **34**: 116–123. *f. 1.* Ja 1944.

Weimer, J. L. Botrytis leaf spot of vetch. Phytopathology **34**: 245–249. *f. 1.* F 1944.

Whetzel, H. H. A new genus of the Sclerotiniaceae. Farlowia **1**: 483–488. *f. 1–6.* Ja 1944.

ECOLOGY AND PLANT GEOGRAPHY

Cain, S. A. Criteria for the indication of center of origin in plant geographical studies. Torreya **43**: 132–154. D 1943 [10 F 1944].

Hutchinson, G. E. Limnological studies in Connecticut. VII. A critical examination of the supposed relationship between phytoplankton periodicity and chemical changes in lake water. Ecology **25**: 3–26. *f. 1–6.* Ja 1944.

McComb, A. L. & Loomis, W. E. Subclimax prairie. Bull. Torrey Club **71**: 46–76. *f. 1–25.* 25 Ja 1944.

Maloney, M. M. Revegetation of coal stripped land near Henryetta, Oklahoma. Proc. Okla. Acad. **22**: 123–129. *f. 1–3.* 1942.

Oosting, H. J. The comparative effect of surface and crown fire on the composition of a loblolly pine community. Ecology **25**: 61–69. Ja 1944.

Pessin, L. J. & Chapman, R. A. The effect of living grass on the growth of longleaf pine seedlings in pots. Ecology **25**: 85–90. Ja 1944.

Williams, R. M. & Oosting, H. J. The vegetation of Pilot Mountain, North Carolina: a community analysis. Bull. Torrey Club **71**: 23–45. *f. 1, 2., t. 1–4.* 25 Ja 1944.

GENERAL BOTANY
(including biography)

Conklin, E. G. Jean Baptiste-Pierre Antoine de Monet, Chevalier de Lamarck. Genetics **29**: [*i–iv*] *port.* Ja 1944.

Dade, H. A. Colour terminology in biology. Mycological Papers **6**: 1–21. *2 charts.* Jl 1943.

Drouet, F. William Albert Setchell. Am. Midl. Nat. **30**: 529–532. N 1943. [Ja 1944].